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A Taxonomic Revision of the South American Species of *Hypolepis* (Dennstaedtiaceae), Part I

Pedro Bond Schwartsburd
Departamento de Biologia Vegetal, Universidade Federal de Viçosa, Av. P.H. Rolfs s.n., Viçosa, MG, Brazil, 36570-900. e-mail: pedro.schw@ufv.br
Jefferson Prado
Instituto de Botânica, Caixa Postal 68041, São Paulo, SP, Brazil, 04045-972.

Abstract.—*Hypolepis* is a subcosmopolitan genus with ca. 80–90 taxa worldwide, and with few taxonomic studies. The present work is a taxonomic revision of the South American species, including Cocos Island (Costa Rica). It has been based, mainly, on the morphological study of nomenclatural types and exsiccates from European and South American herbaria, plus one herbarium from New Zealand and another from the United States of America. Some species were also studied in nature. For South America (incl. Cocos Island), 26 species are here recognized, and a total of 31 taxa (species, subspecies, varieties, and hybrids). Among these are four new taxa: *H. galapagensis*, *H.* ×*glabra*, *H.* ×*paulistana*, and *H. pedropaloensis*. The geographical distribution patterns were classified into nine categories. Minimum and maximum elevations are strong limiting factors of distribution. The taxonomic treatment includes keys to taxa, new and complete synonymies, typifications, taxa description, distribution maps, illustrations, studied material, and taxonomic and/or nomenclatural comments. In addition, there are short discussions about morphology and biogeography.

Key Words.—diversity, ferns, Pteridophyta, South America, taxonomy

Resumo (Portuguese).—*Hypolepis* é um gênero subcosmopolita com ca. 80–90 táxons distribuídos pelo mundo, e com pouquíssimos estudos taxonômicos. O presente trabalho trata da revisão taxonômica das espécies ocorrentes na América do Sul, incluindo a Ilha de Cocos (Costa Rica). O mesmo se desenvolveu, principalmente, através do estudo morfológico dos tipos nomenclaturais e de exsicatas oriundas de herbários europeus e sul-americanos, e de um neo-zeolandês e outro norte-americano. Algumas espécies também foram estudadas em campo. Para a América do Sul (incluindo Cocos) são aqui reconhecidas 26 espécies, e um total de 31 táxons (espécies, subespécies, variedades e híbridos). Destas, quatro são inéditas: *H. galapagensis*, *H.* ×*glabra*, *H.* ×*paulistana* e *H. pedropaloensis*. Os padrões de distribuição geográfica foram classificados em nove categorias. Altitudes mínimas e máximas são fortes fatores limitantes de distribuição. O tratamento taxonômico apresenta chaves de identificação, sinonímias novas e completas, tipificações, descrição dos táxons, mapas de distribuição, ilustrações, material examinado, e comentários taxonômicos e/ou nomenclaturais. Em adição, são apresentadas breves discussões morfológicas e biogeográficas.

Hypolepis Bernh., as currently defined, contains ca. 80(–90) taxa worldwide (including species, subspecies, varieties, and hybrids), and they occur from southern temperate regions of the globe up to northern tropical regions, with a few species extending into northern temperate regions. The genus is characterized by the long-creeping stems with typical solenostelic vascular system, medium-sized to large fronds (up to 10 m long), petioles and rachises commonly armed with aculei, 2-pinnate-pinnatifid to 5-pinnate laminae, lamina indument formed by catenate hairs and sometimes glandular hairs (absence of scales), free veins, marginal or submarginal sori originated at the tip of single veins, and pseudoindusia formed by the recurved lamina margin (or absent in some species). It is now placed in Dennstaedtiaceae, sharing common ancestry with *Monachosorum* Kunze, *Pteridium* Gled. ex Scop., *Paesia* A. St.-Hil., *Blotiella* R.M. Tryon, and *Histiopteris* (Agardh) J. Sm. (Brownsey 1987; Brownsey and Chinnock 1984; Kramer 1990; Mickel and Smith 2004; Moran 1995; Ogura 1972; Smith *et al.* 2008; Schuettpelz and Pryer 2008; Schwartsburd 2012a, 2012b; Schwartsburd and Prado 2014; Tryon and Tryon 1982; Wolf 1995).

History of the genus.—The genus *Hypolepis* was originally described by Bernhardi (1806 [1805]), based solely on *Lonchitis tenuifolia* G. Forst. (= *Hypolepis tenuifolia* (G. Forst.) Bernh.). This plant was collected by Forster in Tanna Island (Brownsey 1987; Forster 1786; Nicolson and Fosberg 2004; Stafleu and Cowan 1976). Thirty years later, Presl (1836) restored and re-circumscribed the genus, ascribing to *Hypolepis* another nine species from the Neotropics, Oceania, and Africa. Among them were the pre-Linnaean *Lonchitis repens* L. (Linnaeus 1753; Plumier 1705), and some species previously ascribed to *Cheilanthes* Sw. In fact, *Hypolepis* and *Cheilanthes* do present a much similar soral morphology: the sori are round, marginal, born at the tip of a single vein, and protected by the recurved lamina (pseudoindusia). Thus, Presl (1836) drew a clearer line between these two genera, adding vegetative characteristics as supplementary diagnostic.

A second addition to the circumscription of *Hypolepis* was done by Smith (1842, 1846), who included *Polypodium rugosulum* Labill. within *Hypolepis.* In this species the sori are submarginal and lack pseudoindusia. Smith's view reinforced the importance of vegetative characteristics for the circumscription of *Hypolepis.* Mettenius (*in* Kunh 1868) reinforced this conception by combining *Polypodium punctatum* Thunb. (another exindusiate species) also in *Hypolepis.*

From the mid 19th to the early 20th centuries, other pteridologists did not fully accept or understand such circumscription for *Hypolepis* (*e.g.,* Christ 1905; Christensen 1906; Diels 1902; Domin 1914; Fée 1852; Hooker 1858, 1862; van Alderwerelt van Rosenburgh 1908). They confused within it a number of pseudoindusiate species currently ascribed to *Adiantopsis* Fée, *Aspidotis* (Hook. & Baker) Copel., *Cheilanthes, Dennstaedtia* Bernh., and *Plecosorus* Fée. And, they regarded *Polypodium punctatum* and *Pol. rugosulum* as belonging to genera currently ascribed to Polypodiaceae, Dryopteridaceae, or Thelypteridaceae, such as: *Dryopteris* Adams., *Nephrodium* Michx., *Phegopteris* (C. Presl) Fée, or *Polypodium* L.

The stele studies of Gwynne-Vaughan (1903) and Bower (1928) suggested once again the inclusion of *Polypodium punctatum* and *Pol. rugosulum* within *Hypolepis.* Finally, Christensen (1913, 1920, 1924, 1925, 1926, 1931, 1932, 1934; Christensen and Skottsberg 1920) presented a new synthetic circumscription for the genus: including *H. punctata* (Thunb.) Mett. and *H. rugosula* (Labill.) J. Sm., and proposing a clearer distinction from *Cheilanthes,* *Aspidotis,* and *Adiantopsis.* Once again, the vegetative characteristics were considered as useful as the soral morphology for the circumscription of *Hypolepis.* Christensen's conception was followed by Ching (1940) and Copeland (1947), and *Hypolepis'* circumscription has stabilized since (*e.g.,* Bronwsey and Chinnock 1984; Kramer 1990; Mickel and Smith 2004; Moran 1995; Schwartsburd 2010, 2012a; Schwartsburd and Prado 2011b, 2014; Tryon and Tryon 1982).

The monophyly of *Hypolepis sensu* Christensen has not yet been rigorously tested. Wolf (1995) demonstrated that *Hypolepis* defined as subcosmopolitan is indeed monophyletic: the three species analyzed strongly grouped together, and they are from Australia, western Samoa, and Ecuador. On the other hand, some authors (*e.g.,* Brownsey 1983; Mickel and Smith 2004) questioned the monophyly of the genus, due especially to the current inclusion of two strange species: *H. nigrescens* Hook. and *H. distans* Hook. These two species present some consistent morphological differences (in comparison to most species), and their chromosome numbers are respectively $n = 29$ and $n = 28$, while the usual numbers for *Hypolepis* are $n = 52$ and $n = 104$, from an hypothetical ancestor with $n = 26$ (Brownlie 1957; Brownsey 1983; Manton and Vida 1968; Smith and Mickel 1977).

There is no monograph of the genus, and circumscription of species has commonly been problematic — see, for example, the comments of Tryon and Tryon (1982:400), Proctor (1989:177), Tryon and Stolze (1989:109), Kramer (1990:88), Moran (1995:153), Mickel and Smith (2004:353), and Kessler and Smith (2007:194). The leading works on the genus are the local taxonomic revisions done by Brownsey and Chinnock (1984, 1987), Biswas (1985), and Bronswey (1987). Recent works of Flora also contribute to its understanding (*e.g.,* Cremers and Kramer 1991; Mickel and Smith 2004; Moran 1995; Murillo-Pulido *et al.* 2008; Ponce *et al.* 2008; Proctor 1989; Rodríguez 1995; Tryon and Stolze 1989). Finally, the novelties recently presented by Schwartsburd and Prado (2009, 2011a, 2011b, 2014), Schwartsburd (2010, 2012a, 2012b), Schwartsburd *et al.* (2012), and Arana *et al.* (2014) also promoted a clearer view of the genus and its species.

MATERIALS AND METHODS

We analyzed material from the the following herbaria: ALCB, B, BAB, BCN, BCRU, BHCB, BM, BR, CAY, CORD, EAC, ESA, HAS, HB, HBR, HRB, HRCB, HUA, HUCS, HUEFS, HVASF, FI, FI-PS, FI-W, G, ICN, IPA, K, L, LP, LE, LECB, LPB, MBM, MPUC, MVFQ, MVJB, MVM, MY, OUPR, OXF, PEUFR, PR, PRC, RB, SI, SMDB, SP, SPF, U, UCS, UFP, UPCB, UPS, US, VEN, VIC, W, and WELT. All specimens cited were personally studied, otherwise they are indicated: "*n.v.*" (not seen). An exclamation mark (!) in the type collections indicates we personally saw them; otherwise they are marked as "*n.v.*" or "image!" (whenever their images online were observed).

The full list of the specimens examined is available in Schwartsburd's Dissertation (2012b), and the contracted form in Appendix 3. In the taxonomic treatment only one specimen per state or department is cited, except for the taxa with few collections. Field trips were made within the eastern region of Brazil. The following taxa were personally studied in nature: *Hypolepis acantha, H. mitis, H.* ×*paulistana, H. repens, H. rugosula* subsp. *pradoana, H. stolonifera* var. *stolonifera, H. stolonifera* var. *delasotae,* and *H. stolonifera* var. *nebularis*. The main collections resulted from our field trips are deposited in SP and VIC herbaria, with duplicates sent to others.

To construct the maps, we estimated most of the coordinates searching in Google^{TM} Earth. Maps were drawn using Diva-Gis, version 7.5 (Hijmans 2013), using elevation and administrative layers. The layers were obtained from its website. For most countries, only the 'country level' was used, except for Brazil, Argentina and U.S.A., in some cases, for which the 'state' (or 'department') level was also used. The altitudinal layers were manually patronized into five levels in gray scale: white (sea level to 1000 m), light gray (1000–2000 m), gray (2000–3000 m), dark gray (3000–4000 m), and black (> 4000 m).

Most of morphological terms follow Lellinger (2002). Anatomical studies were done using materials preserved in 50% FAA, then in 70% alcohol. Sections were made manually. Dehydration and staining followed methods in Johansen (1940) and Sass (1951). The dyes used were astra blue and safranin, at 9:1 (Bukatsch 1972). Microscopic photos were taken using an Olympus®, model BX41, with Motic® camera, model Moticam 2500, 5.0 MP resolution. Two specimens belonging to the following species were analyzed: *Hypolepis acantha* (*Schwartsburd 2264*), *H. repens* (*Schwartsburd 2335*), *H. rugosula* subsp. *pradoana* (*Schwartsburd 2310*), and *H. stolonifera* var. *stolonifera* (*Labiak 4269*). The sections were made of medial regions of the stems, and proximal and distal regions of the petioles. Images under steresocope were taken in a trinocular stereoscope Coleman®, model NSZ 606T, with camera and screen attached (Coleman® NLCD – pad 1), and with a 2x objective lens attached. Illustrations were made by K. R. Sousa; and one (Fig. 12) by R. Pinto, based on earlier drawings by the senior author and P. Davies (from K). The species in the taxonomic treatment are presented in alphabetic order. The authors of scientific names are abbreviated according to Pichi-Sermolli (1986), with additions from the International Plant Names Index (IPNI) website.

Results and Discussion

Diversity and distribution.—The species ascribed to *Hypolepis* occur in most continental land masses and oceanic islands. The extant distribution of the genus is best classified as subcosmopolitan: more specifically, the species occur in southern temperate regions, southern tropical regions, equatorial regions, northern tropical regions, and a few of them also in northern temperate regions (*e.g.,* Brownsey and Chinnock 1984; Kramer 1990; Schwartsburd and Prado 2014; Tryon and Tryon 1982). In the southern regions they reach as south as 52.5°S in Oceania (Campbell Island), and 49°S in South America (Brownsey and Chinnock 1984; Schwartsburd and Prado 2014) (Fig. 2). On the other hand, the northern limits of the genus are lower: they reach Japan and China in Asia (Shieh 1994), and Florida and Mexico in North America (Mickel and Smith 2004; Naumann 1993) (*e.g.,* Fig. 22C). The genus is absent in Europe. In tropical and equatorial regions the genus is also absent in semi-desert or desert regions, such as in Saharan Africa (Alston 1959; Roux 2009; Schelpe 1970; Verdcourt 2000), central Australia (Brownsey and Chinnock 1987), and the Dry Diagonal in South America (Fig. 2).

The extant distribution of the genus, and the presumed age of Dennstaedtiaceae (Schneider *et al.* 2004; Serbet and Rothwell 2003), suggest a Gondwanic origin of the genus, and further vicariance from its break up (Lovis 1959; Schwartsburd and Prado 2014) — although some authors prefer to interpret the distribution of *Hypolepis* based on dispersal (Browlie 1962; Brownsey 2001; Parris 2001). The occurrence in northern regions and volcanic oceanic islands are probably due to secondary dispersal events.

Regarding species distributions, some of them are narrow endemics, such as *Hypolepis galapagensis* endemic to the Galapagos (Fig. 10B), and *H. krameri,* endemic to the Mount Roraima region (Fig. 11C), and some of them are widespread. *Hypolepis repens,* for example, occur in nearly the whole Neotropical region (Fig. 22C). The intriguing subcomopolitan distribution of *H. rugosula* was studied in detail by Schwartsburd and Prado (2014).

Previous estimates for species richness within the genus were about 40–45 species (Kramer 1990; Mickel and Smith 2004; Tryon and Tryon 1982). Recently, Schwartsburd (2012) and Arana *et al.* (2014) mentioned around 80 taxa. We estimate that there are ca. 80–90 *Hypolepis* taxa (species, subspecies, varieties, and hybrids) in the World, of which ca. 40–45 occur in the Americas, ca. 30–35 in Oceania and Asia, only ca. 5 in Africa, one/two per most oceanic islands (some of them endemics), and none in Europe. In South America (plus Cocos Island) 26 species occur, and a total of 31 taxa. Table 1 shows the South American countries and the *Hypolepis* taxa occurring there.

In South America, the areas with higher species richness and endemism correspond to those indicated by Tryon (1972, 1986): Guianan shield, Andean, and southeastern Brazil. Among the South American countries, the genus is absent only in Uruguay. We categorized the South American taxa (incl. Cocos Island) into nine patterns of distribution:

1. *Neotropical* — widespread species, occurring nearly throughout the Neotropics: *Hypolepis repens* (Fig. 22C) and *H. rigescens* (Fig. 23A);
2. *Western Neotropical* — widespread species, occurring in the western side of the Neotropics: *Hypolepis nigrescens* (Fig. 17A);
3. *Circum-Caribbean Sea* — species occurring around the Caribbean sea, especially in southern Mexico, Mesoamerica, Antilles, Colombia, and/or Venezuela: *Hypolepis melanochlaena* (Fig. 14B), *H. nuda* (Fig. 17B), *H. stuebelii* (Fig. 25B), and *H. viscosa* (Fig. 26);
4. *Amazonian* — species occurring in the Amazon Forest, in low elevations: *Hypolepis hostilis* (Fig. 11B);
5. *Mount Roraima* — species narrow endemics to the Mount Roraima region (intersection of Venezuela, Guyana, and northern Brazil): *Hypolepis guianensis* (Fig. 11A), *H. krameri* (Fig. 11C), and *H. trinationalis* (Fig. 25C);

6. *Andean* — species occurring in the high lands of the Andes and sometimes extending onto the high lands of Mesoamerica: *Hypolepis bogotensis* (Fig. 7B), *H. crassa* (Fig. 7C), *H. flexuosa* (Fig. 10A), *H.* ×*glabra* (Fig. 10C), *H. obtusata* (Fig. 17C), *H. parallelogramma* (Fig. 20A), *H. pedropaloensis* (Fig. 20C), *H. pteroides* (Fig. 22B), and *H. scandens* (Fig. 23C);
7. *Islanders* — species endemic to Galapagos and Cocos Islands, respectively: *Hypolepis galapagensis* (Fig. 10B) and *H. lellingeri* (Fig. 14A);
8. *Brazilian Atlantic Forest* — species occurring in the Atlantic Forest of southern and southeastern Brazil, and sometimes extending onto southern Bahia or northeastern Argentina: *Hypolepis acantha* (Fig. 7A), *H. mitis* (Fig. 14C), *H.* ×*paulistana* (Fig. 20B), *H. rugosula* subsp. *pradoana* (Fig. 23B), *H. stolonifera* var. *stolonifera* (Fig. 25A), *H. stolonifera* var. *delasotae* (Fig. 25A), and *H. stolonifera* var. *nebularis* (Fig. 25A);
9. *Austral* — species occurring in the Austral region of South America, more or less in the *Southern Cone,* reaching as far south as 49°S, and one of them also in Juan Fernandez and Chiloé Islands: *Hypolepis poeppigii* (Fig. 22A) and *H. rugosula* subsp. *poeppigiana* (Fig. 23B).

In South America, *Hypolepis* taxa occur from sea level to ca. 4,600 m in elevation. Each taxon has its own altitude distribution, marked by minimum and maximum elevations (Fig. 1). Most taxa are terricolous, but a few grow in crevices between rocks (*e.g., Hypolepis rugosula, H. crassa, H. obtusata, H. trinationalis*). Most species seen in nature grew in partial shade, such as forests borders, clearings, or caves, and they also tend to frequent moist soils.

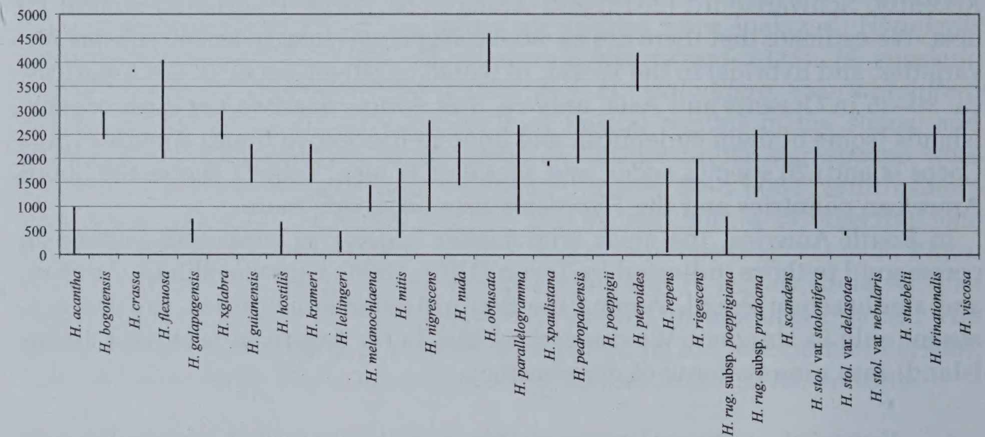

FIG. 1. Elevational ranges (in meters) of *Hypolepis* taxa from South America and Cocos Island.

MORPHOLOGY

Hypolepis species are commonly big plants, with horizontal branching rhizomes, reaching dozens of meters long, and leaves up to 10 m long. Due to the large size of the plants, herbarium material is mostly fragmentary, composed of one or a few pieces of a frond. Thus, in order to completely understand their morphology, habit, and autecology, they must also be studied

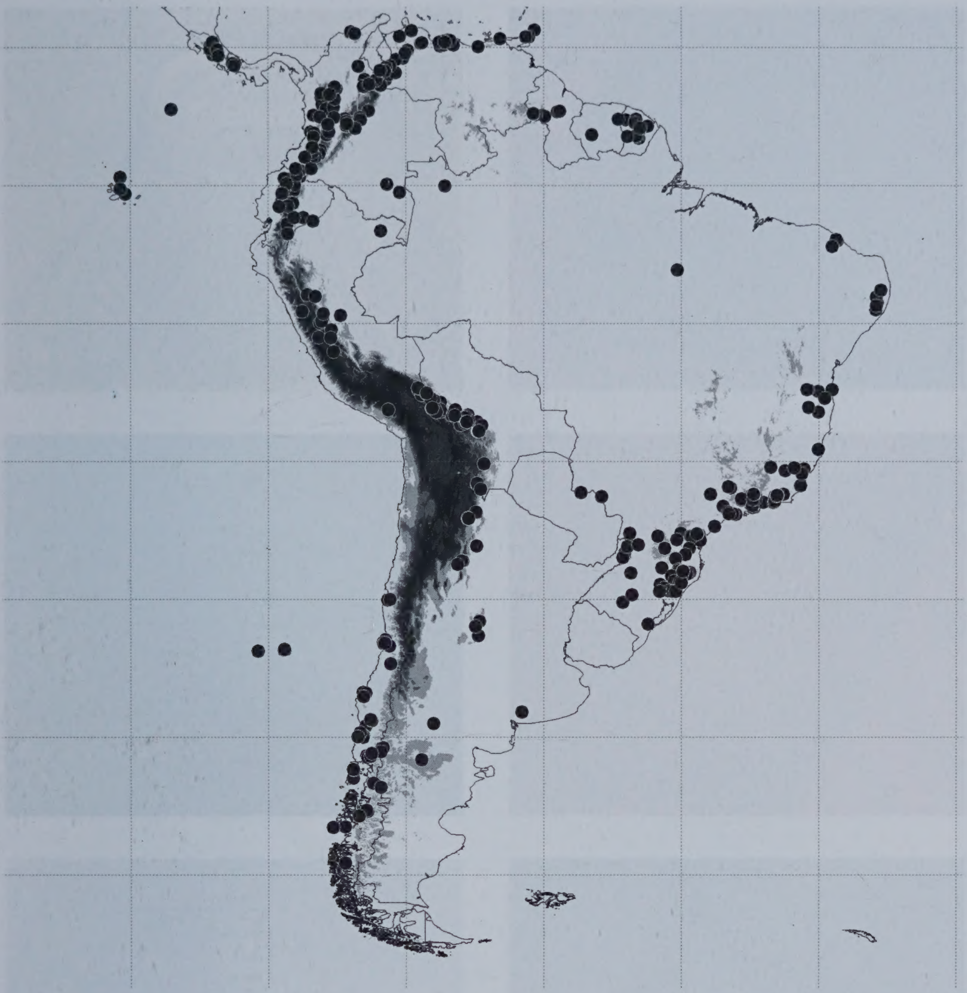

FIG. 2. Distribution of *Hypolepis* in South America and Cocos Island

in the field (see also Brownsey and Chinnock 1984; Moran 1995). In contrast to the large species, *H. bogotensis, H. crassa, H. obtusata,* and *H. pteroides* are small plants, and herbarium material is generally complete.

Stems and habit.—In *Hypolepis,* as in nearly all genera of the Dennstaedtiaceae, the stems are usually horizontal, long-creeping, branched, and mostly subterranean, and thus called rhizomes (Figs. 5A, B). They appear to have indeterminate growth potential. This branching ability is responsible for forming an extensive rhizome net and so it is quite hard to differentiate individuals within a population. A studied carried out by Gruber (1981), showed an example of how big one individual of *H. repens* can get, with a rhizome 30 m long, occupying an area of 13 m^2, and bearing more than 50

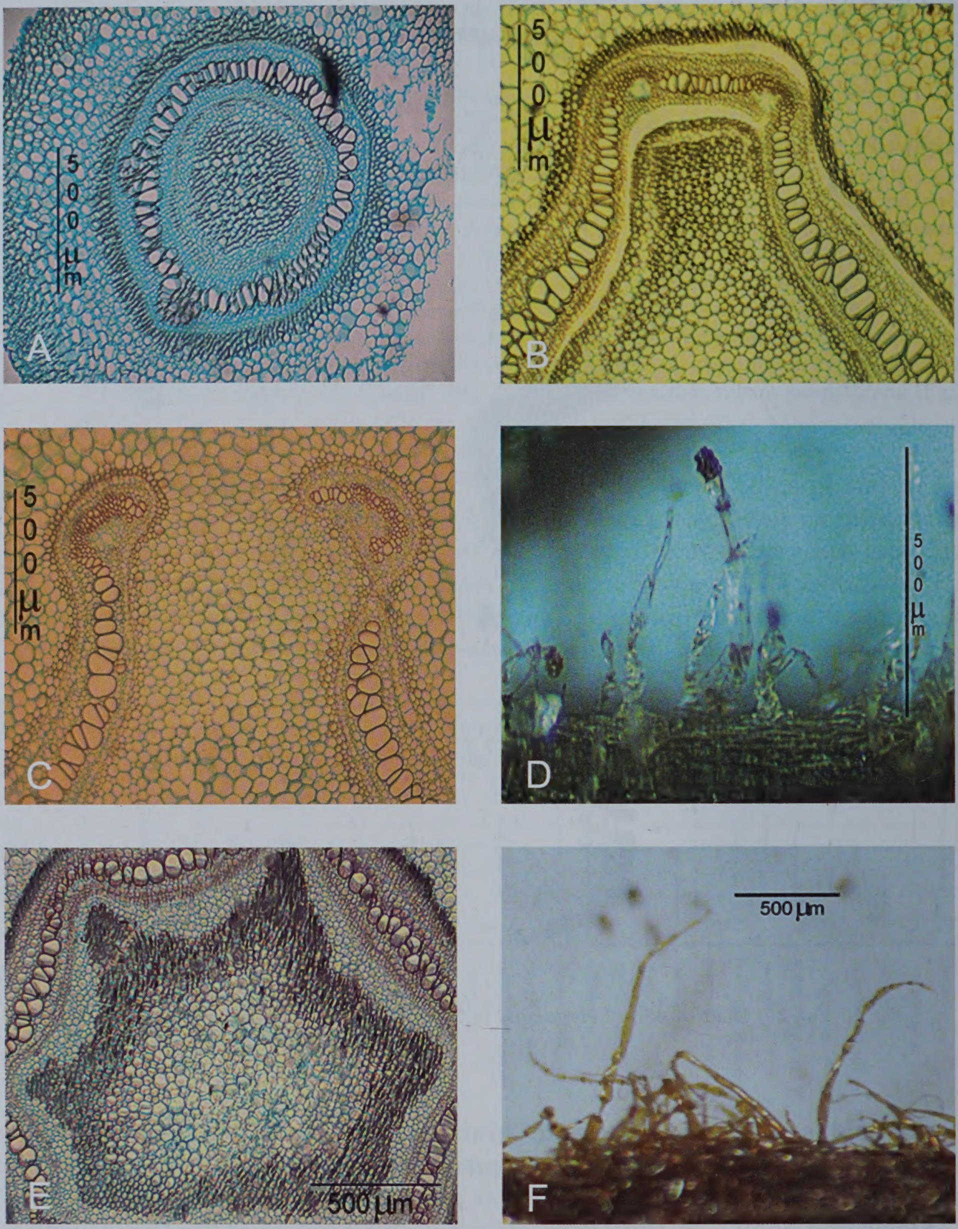

FIG. 3. A–D. *Hypolepis rugosula* subsp.*pradoana*. A. Rhizome in cross section, showing the stele (*Schwartsburd 2310*). B. Proximal region of the petiole in cross section, showing the π-shaped vascular bundle (*Schwartsburd 2310*). C. Distal region of the petiole in cross section, showing two vessels (*Schwartsburd 2310*). D. Catenate-glandular hairs from pinna-rachis, seen under stereoscope (*Schwartsburd 2323*). E, F. *Hypolepis stolonifera* var. *stolonifera*. E. Rhizome in cross section, showing the stele (*Labiak 4269*). F. Hairs of the rhizome, seen under stereoscope (*Schwartsburd 1369*).

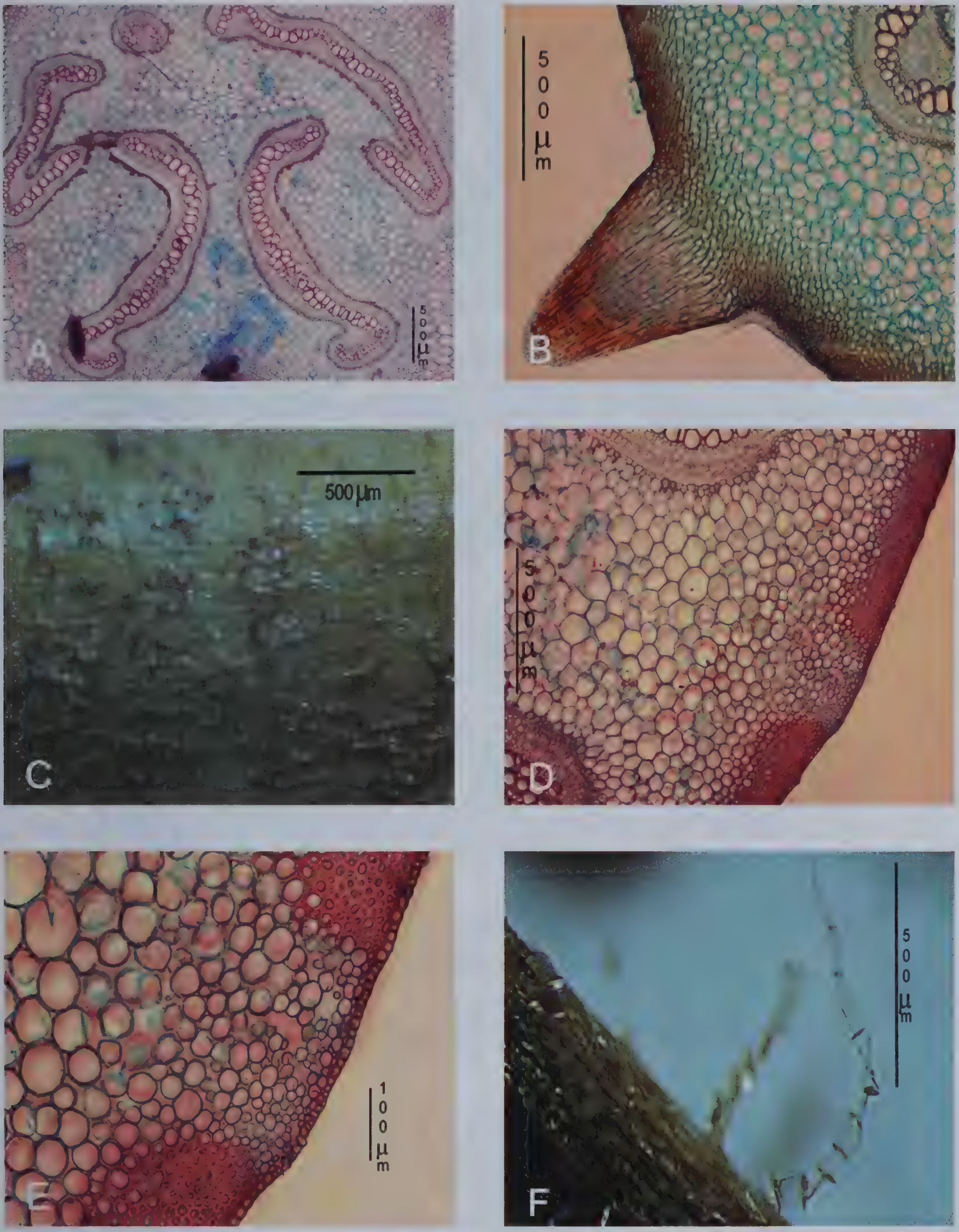

FIG. 4. A–C. *Hypolepis repens.* A. Proximal region of the petiole in cross section, showing the Ω-shaped vascular bundle (*Schwartsburd 2335*). B. Distal region of the petiole in cross section, showing the cortex and a aculeous (*Schwartsburd 2335*). C. Trichomidia from rachis, seen under stereoscope (*Schwartsburd 2510*). D–F. *Hypolepis stolonifera* var. *stolonifera.* D. Proximal region of the petiole in cross section, showing the outer cortex (*Labiak 4269*). E. Proximal region of the petiole in cross section, showing the line of aerophore in detail (*Labiak 4269*). F. Catenate-acicular hairs from pinna-rachis, seen under stereoscope (*Schwartsburd 1369*).

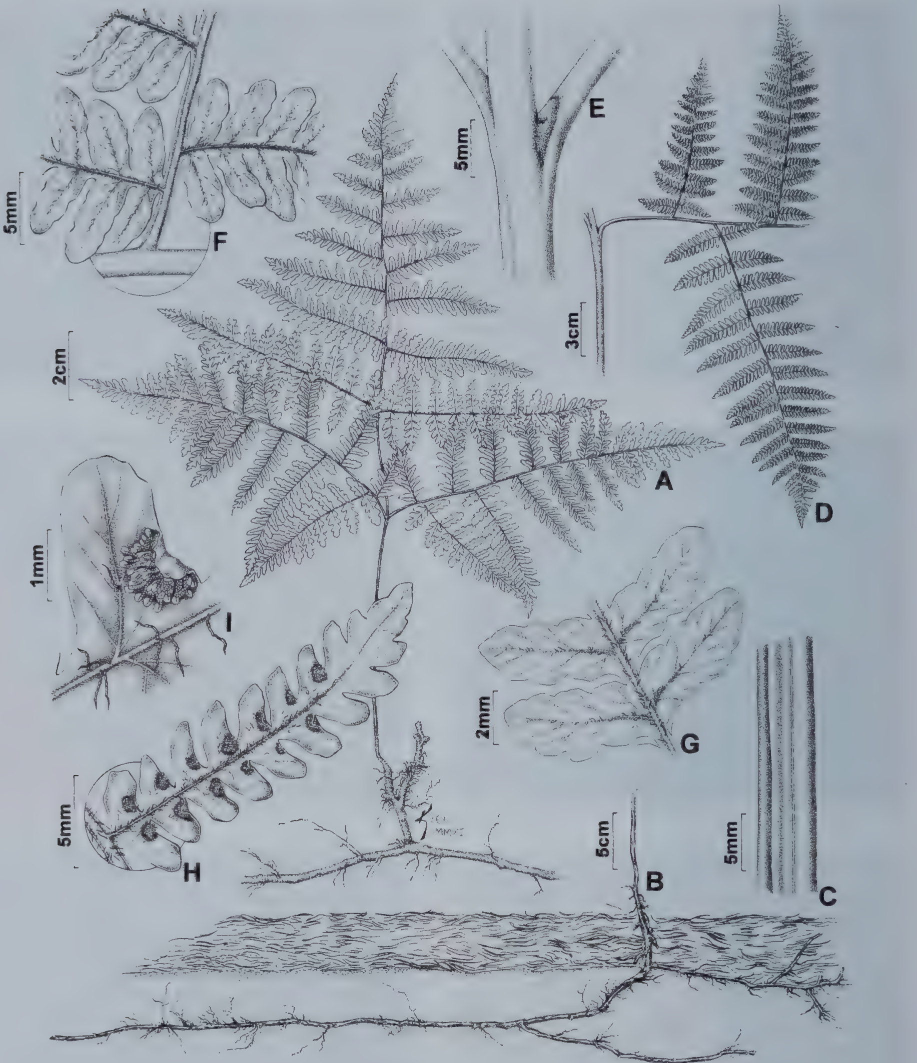

Fig. 5. *Hypolepis stolonifera* var. *stolonifera*. A. Habit of a small frond (*Schwartsburd 1369*). B. Habit of the rhizome (*Schwartsburd 2209*). C. Petiole proximally, showing adaxial groove and line of aerophore (*Schwartsburd 1426*). D. Basal pinna (*Schwartsburd 1928*). E. Intersection of petiole, rachis, and pinna-rachises, abaxially (*Schwartsburd 1928*). F. Pinnules, abaxially (*Schwartsburd 1928*). G. Segments, abaxially (*Schwartsburd 1928*). H. Fertile pinnule, abaxially (*Labiak 4429*). I. Fertile segment, abaxially, showing detail of sorus and pseudoindusium (*Labiak 4429*).

leaves (croziers, developed leaves, and dead leaves). In some species the leaves are borne close to each other, and the individual gets the thicket-forming habit.

The vascular system of the stem in *Hypolepis* is the dorsiventral typical solenostele (Figs. 3A, E), in which there is one continuous, tubular,

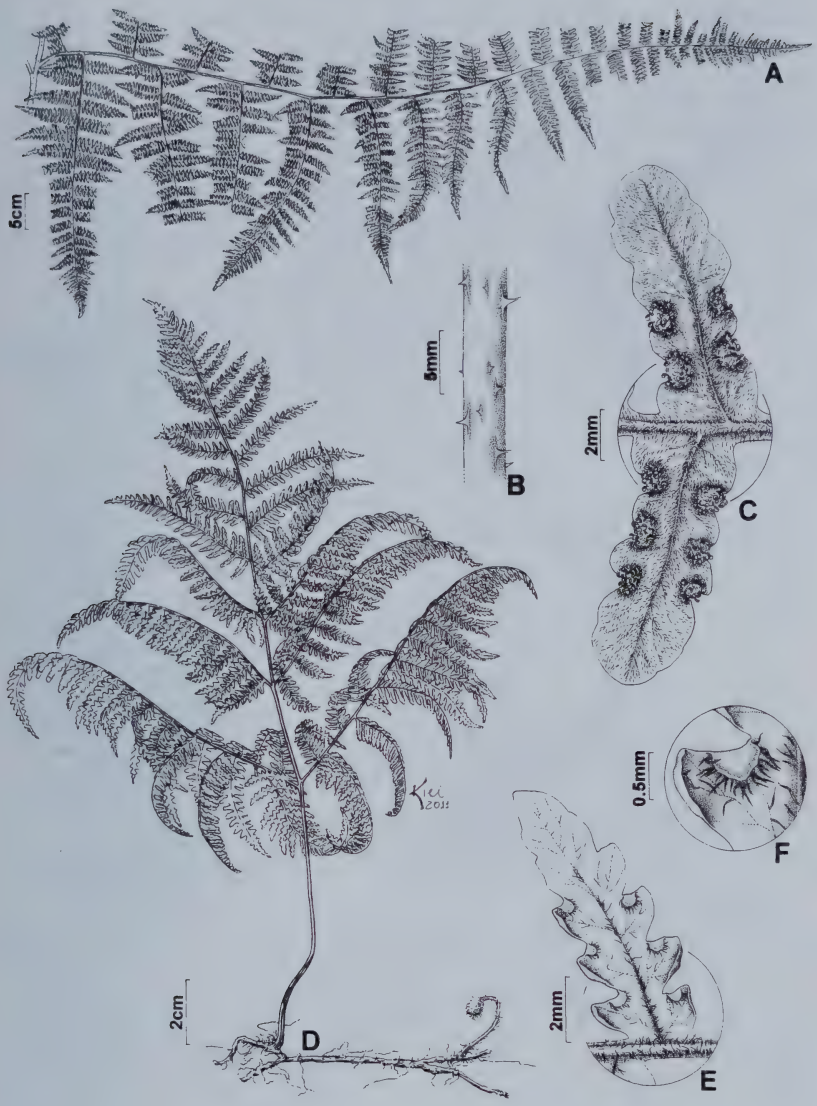

FIG. 6. A–C *Hypolepis acantha* (*Schwartsburd 1344*). A. Basal pinna. B. Rachis, showing aculei. C. Segments, abaxially. D–F *Hypolepis stolonifera* var. *nebularis.* D. Habit of a small frond (*Labiak 4433*). E. Segment, abaxially (*Schwartsburd 2309*). F Segment, abaxially, showing detail of sorus and pseudoindusium (*Schwartsburd 2309*).

amphiphloic stele, interrupted at the leaf traces, enclosing a pith, and bearing alternate leaves in the dorsi-lateral side (Gwynne-Vaughan 1903; Ogura 1972). Other Dennstaedtiaceae genera also present solenostelic stems, such as *Microlepia* and *Histiopteris*. On the other hand, other genera present different steles, such as *Pteridium* (two cycles of perforated dictyosteles) and the group of *Dennstaedtia dissecta* (solenostele with an inner protuberance; or polyciclic solenostele) (Ogura 1972; pers. obs. of the authors).

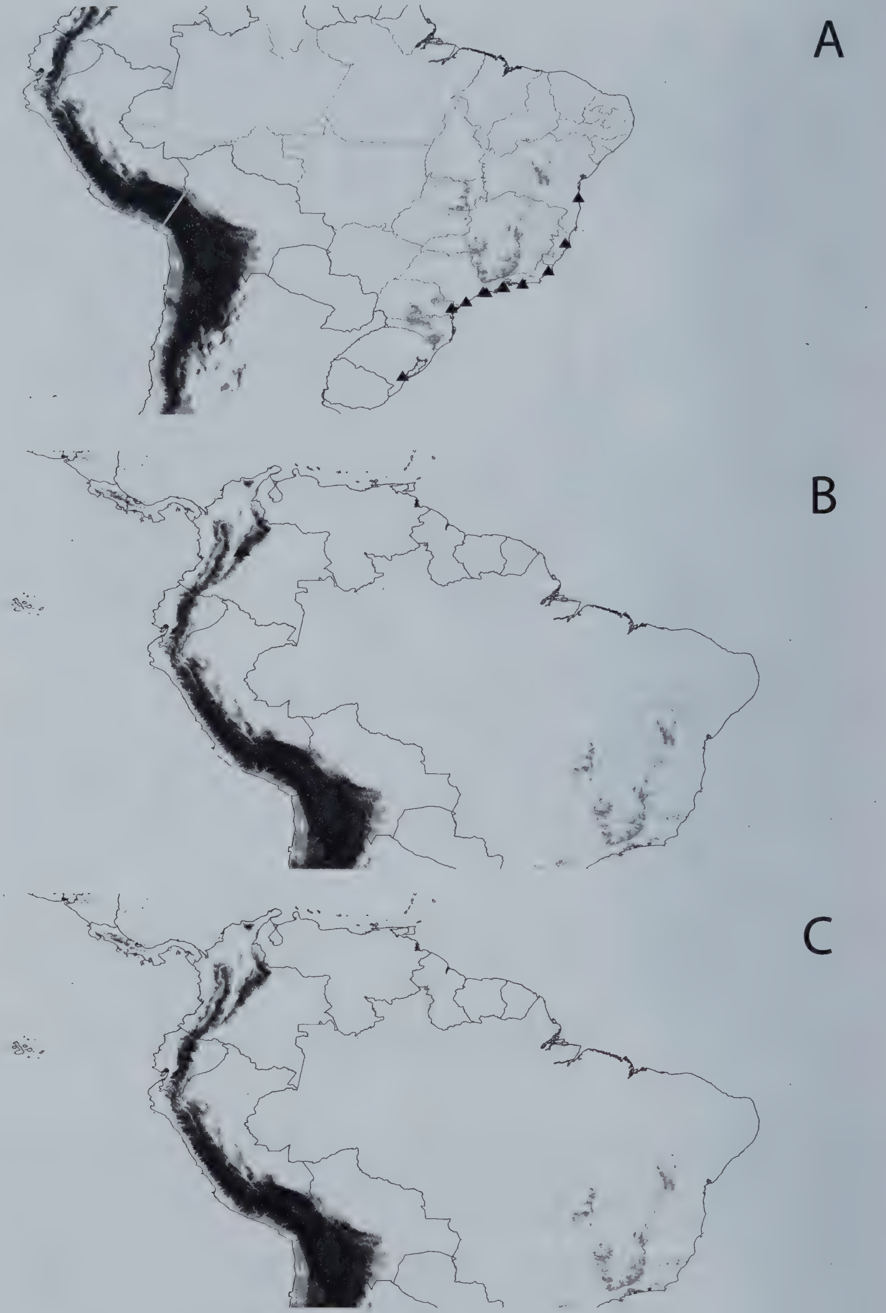

FIG. 7. A. Distribution of *Hypolepis acantha*. B. Distribution of *Hypolepis bogotensis*. C. Distribution of *Hypolepis crassa*.

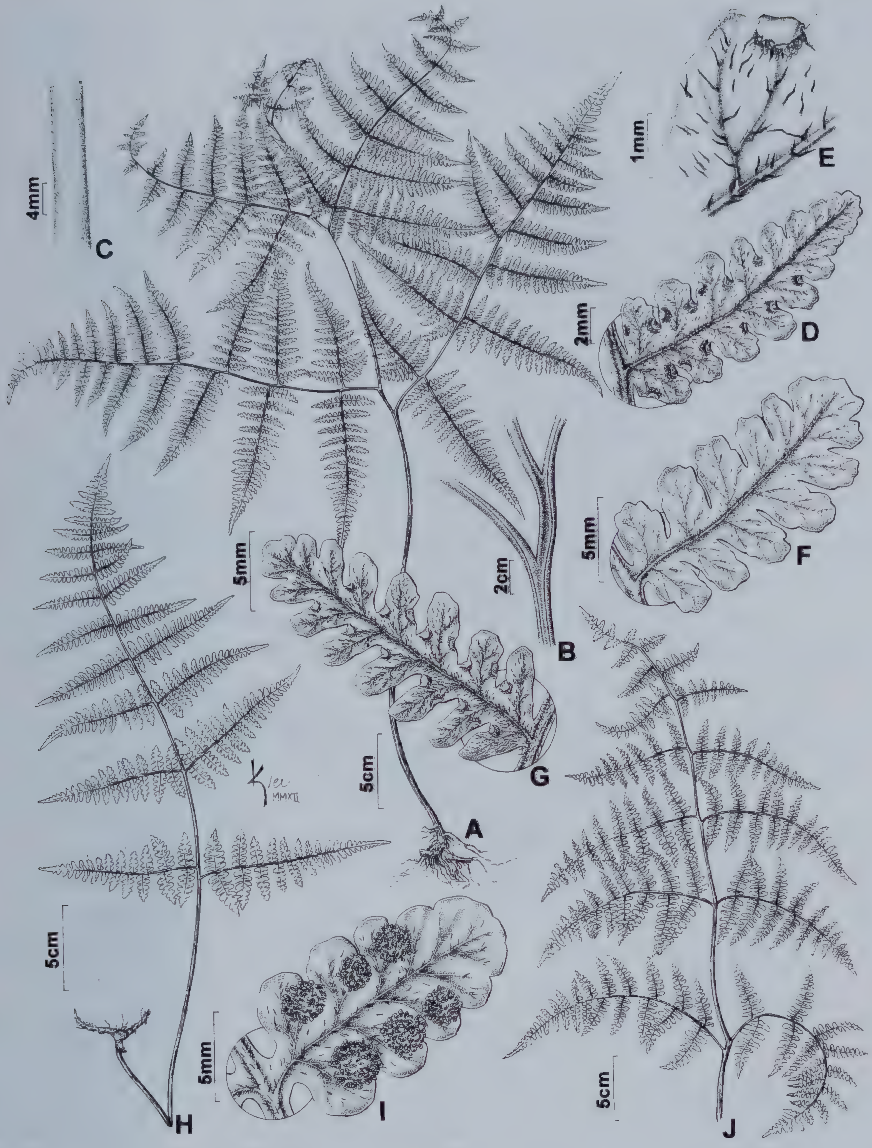

FIG. 8. A–G *Hypolepis flexuosa*. A. Habit of a small frond (*Beck 1435*). B. Intersection of petiole, rachis and pinna-rachis, adaxially (*Kessler 6776*). C. Detail of a petiole (*Lehmann 4441*). D. Fertile secondary pinnule, abaxially (*Beck 1435*). E. Fertile segment, abaxially, showing detail of sorus and pseudo-indusium (*Beck 1435*). F. Secondary pinnule, abaxially (*Kessler 9331*). G. Fertile secondary pinnule, abaxially (*Solomon 16418*). H, I *Hypolepis bogotensis* (*Lindig 224*). H. Habit. I. Pinnule, abaxially. J. *Hypolepis* ×*glabra* (*Karsten s.n.*), habit.

Among the species studied, we found two shapes of the pith and stele: those with terete steles and pith, found in *Hypolepis rugosula* subsp. *pradoana* (Fig. 3A), and those with stellar shaped steles and pith, as found in *H. acantha* and *H. stolonifera* var. *stolonifera* (Fig. 3E). The species studied also present

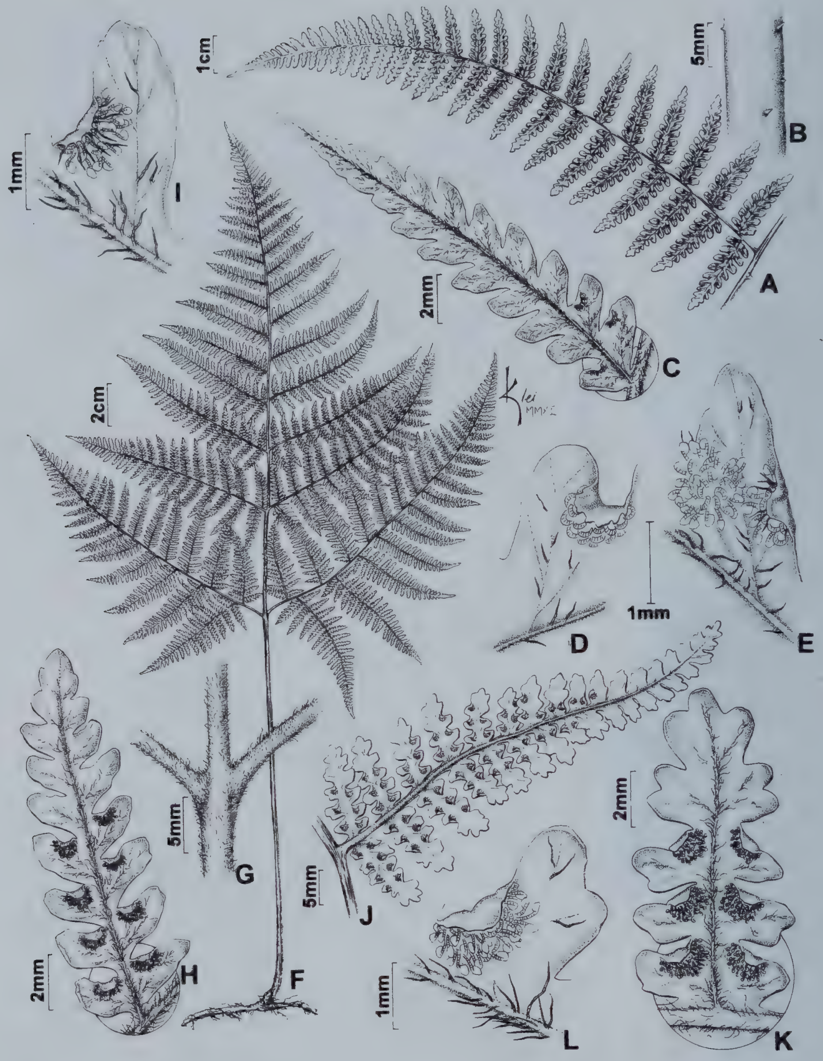

FIG. 9. A–E *Hypolepis mitis*. A. Pinnule, abaxially (*Schwartsburd 2317*). B. Petiole, showing aculei (*Schwartsburd 2317*). C. Secondary pinnule, abaxially (*Gardner 199*). D. Fertile segment, abaxially, showing detail of sorus and pseudoindusium (*Schwartsburd 2317*). E. Fertile segment, abaxially, showing detail of sori and pseudoindusia (*Schwartsburd 2317*). F–I *Hypolepis ×paulistana* (*Schwartsburd 2298*). F. Habit. G. Intersection of petiole, rachis, and pinna-rachises, abaxially. H. Secondary pinnule, abaxially. I. Fertile segment, abaxially, showing detail of sorus and pseudoindusium. J–L *Hypolepis crassa* (*Øllgaard 8155*). J. Basal pinna. K. Pinnule, abaxially. L. Fertile segment, abaxially, showing detail of sorus and pseudoindusium.

an external ring of schlerenchymatous cells surrounding the main vascular bundle (Figs. 3A, E).

Some species of *Hypolepis* bear two lateral lines of aerophores in their stems. Such lines have mostly been recorded for petioles in other ferns (Davies

TABLE 1. Distribution of *Hypolepis* in South America (and Cocos Island) per country. Endemics in boldface.

Country	Number of taxa (number of endemics)	Taxa
Cocos Island (Costa Rica)	1 (1)	***H. lellingeri***
Colombia	14 (3)	***H. bogotensis***, *H. flexuosa*, ***H. ×glabra***, *H. hostilis*, *H. nigrescens*, *H. nuda*, *H. obtusata*, *H. parallelogramma*, ***H. pedropaloensis***, *H. pteroides*, *H. repens*, *H. rigescens*, *H. stuebelii*, *H. viscosa*
Venezuela	13 (0)	*H. flexuosa*, *H. guianensis*, *H. hostilis*, *H. krameri*, *H. melanochlaena*, *H. nigrescens*, *H. nuda*, *H. parallelogramma*, *H. repens*, *H. rigescens*, *H. stuebelii*, *H. trinationalis*, *H. viscosa*
Guyana	7 (0)	*H. guianensis*, *H. hostilis*, *H. krameri*, *H. nigrescens*, *H. repens*, *H. rigescens*, *H. trinationalis*
Suriname	3 (0)	*H. hostilis*, *H. repens*, *H. rigescens*
French Guiana (France)	2 (0)	*H. hostilis*, *H. repens*
Ecuador	10 (2)	***H. crassa***, *H. flexuosa*, *H. hostilis*, *H. obtusata*, *H. parallelogramma*, *H. pteroides*, *H. repens*, *H. rigescens*, *H. stuebelii*
(Galápagos)		***H. galapagensis***
Peru	8 (0)	*H. flexuosa*, *H. hostilis*, *H. nigrescens*, *H. obtusata*, *H. parallelogramma*, *H. pteroides*, *H. rigescens*, *H. stuebelii*
Bolivia	9 (1)	*H. flexuosa*, *H. hostilis*, *H. nigrescens*, *H. obtusata*, *H. parallelogramma*, *H. poeppigii*, *H. repens*, *H. rigescens*, ***H. scandens***
Brazil	14(5)	***H. acantha,*** *H. guianensis*, *H. hostilis*, *H. krameri*, ***H. mitis,*** *H. nigrescens*, ***H. ×paulistana***, *H. repens*, *H. rigescens*, ***H. rugosula*** subsp. ***pradoana,*** *H. stolonifera* var. *stolonifera*, *H. stolonifera* var. *delasotae*, ***H. stolonifera*** var. ***nebularis,*** *H. trinationalis*
Paraguay	1 (0)	*H. repens*
Uruguay	0	
Chile	2 (0)	*H. poeppigii*, *H. rugosula* subsp. *poeppigiana*,
(Juan Fernandez Islands)		*H. rugosula* subsp. *poeppigiana*,
(Chiloé Islands)		*H. rugosula* subsp. *poeppigiana*
Argentina	4 (0)	*H. poeppigii*, *H. rugosula* subsp. *poeppigiana*, *H. stolonifera var. stolonifera*, *H. stolonifera* var. *delasotae*

1991; Ogura 1972). They are originated in the stems, and they continue onto the petioles, rachises, and sometimes also on the pinna-rachises — the details of the lines of aerophores are better presented below, under the section *Petioles and Rachises.*

The indument of the stems is always formed of multi-cellular catenate-acicular hairs. The hairs are brown (ranging from yellowish to reddish-brown), linear, with one row of cells, and never furcate or stellate (Fig. 3F). The hairs are typically 1–3 mm long and composed of 10–25 cells (shorter in *Hypolepis flexuosa*). In living material the hairs are rigid, with a more or less elongate

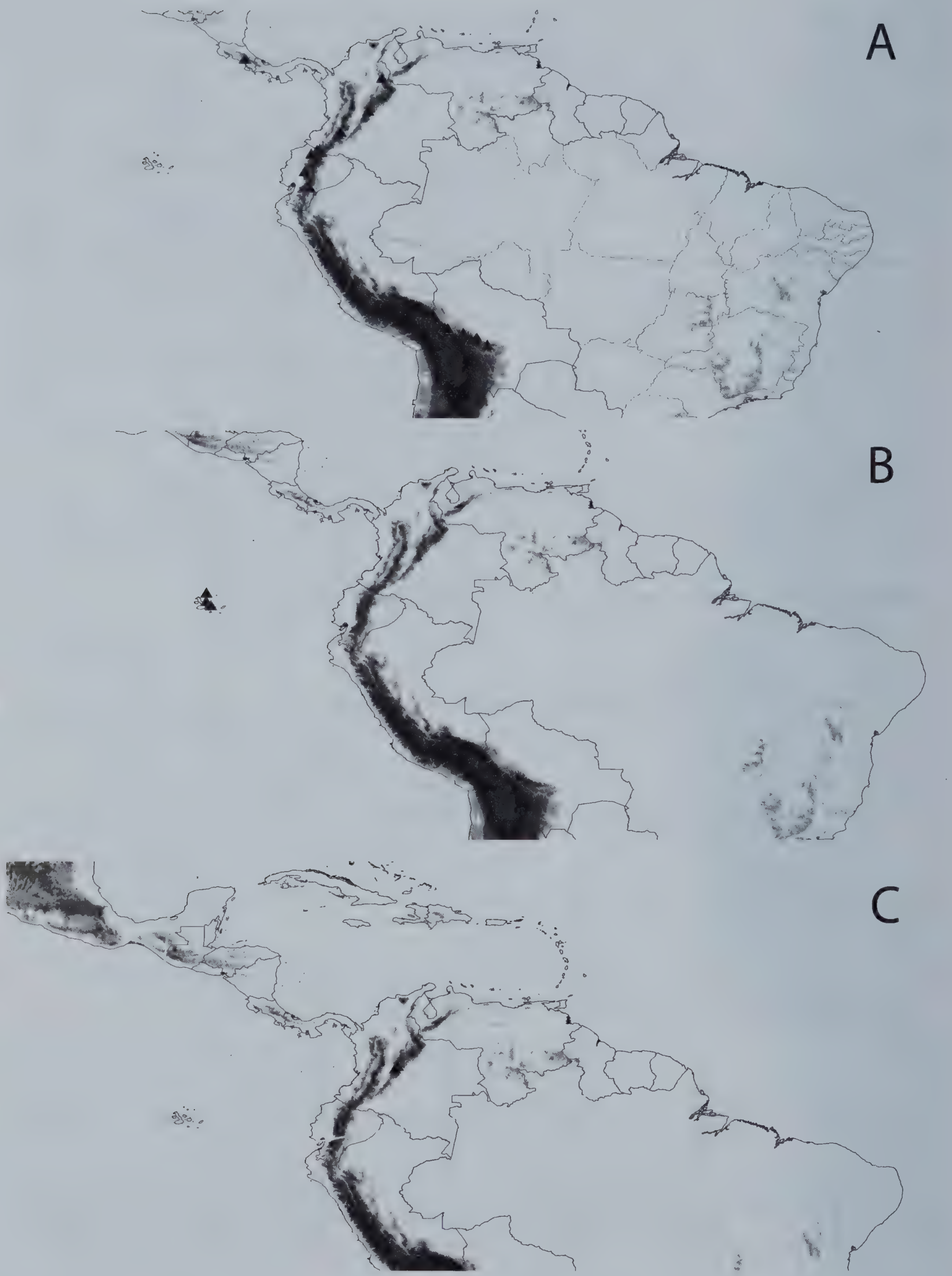

FIG. 10. A. Distribution of *Hypolepis flexuosa*. B. Distribution of *Hypolepis galapaguensis*. C. Distribution of *Hypolepis* ×*glabra*.

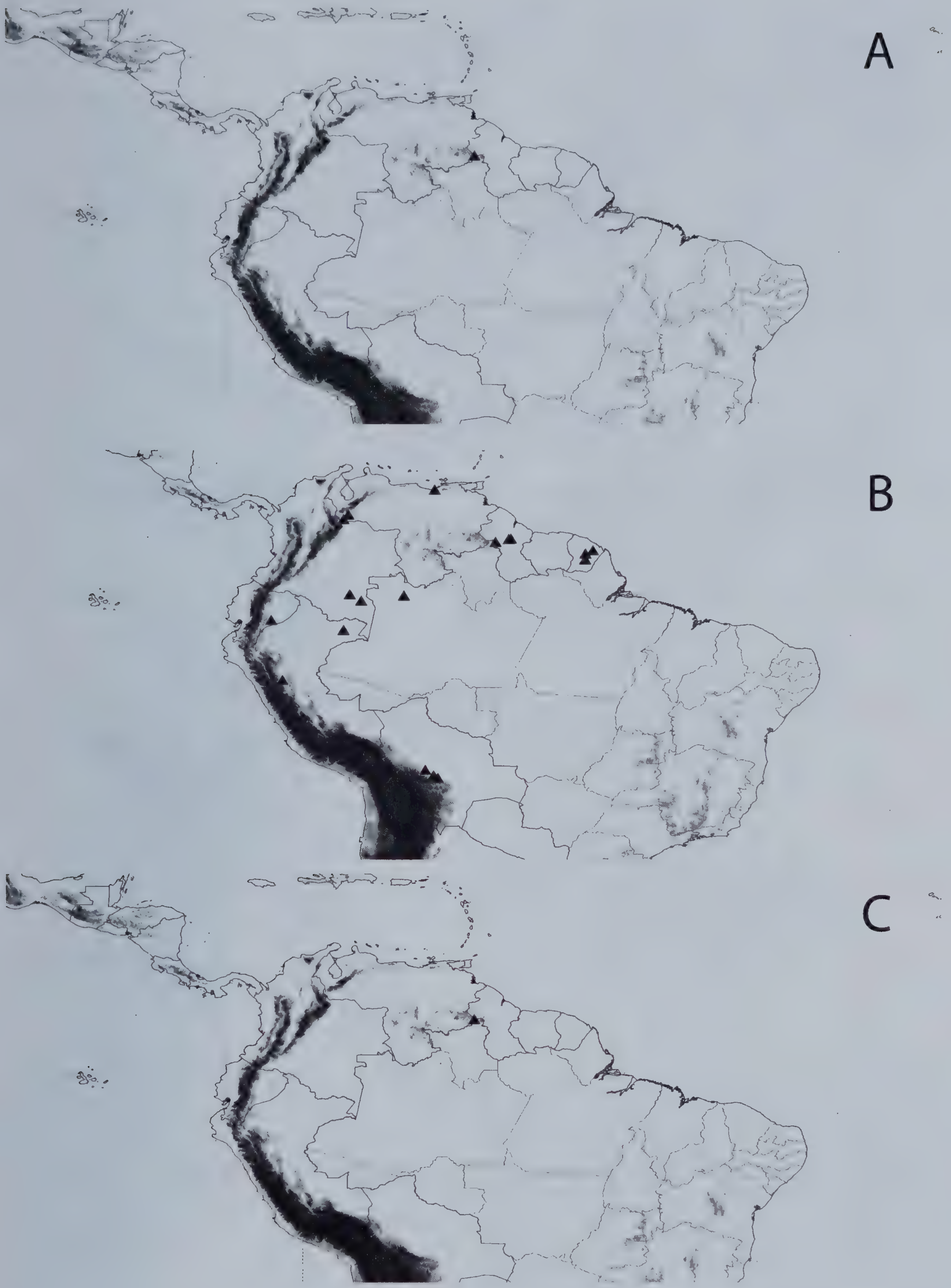

FIG. 11. A. Distribution of *Hypolepis guianensis.* B. Distribution of *Hypolepis hostilis.* C. Distribution of *Hypolepis krameri.*

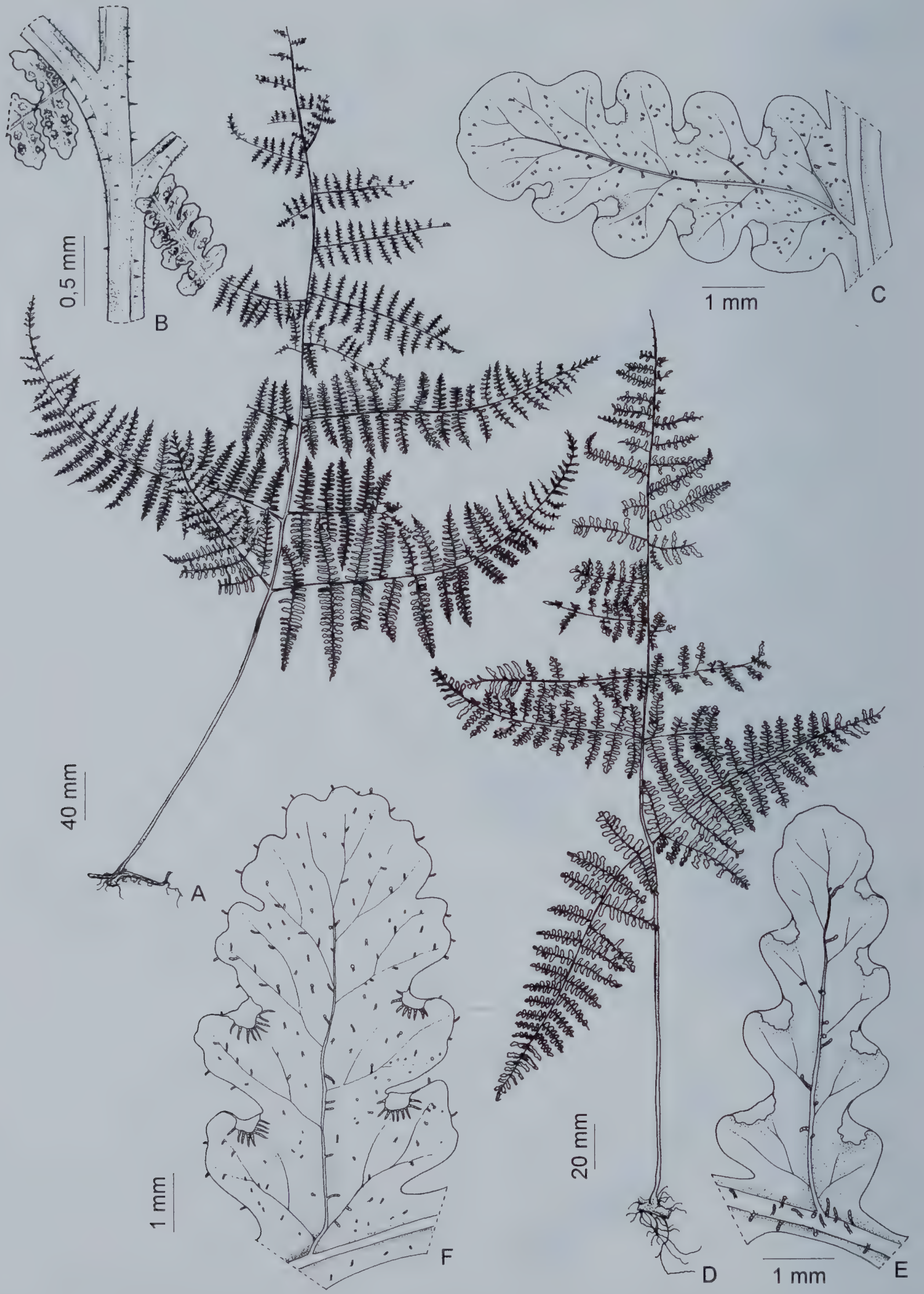

FIG. 12. A–C *Hypolepis rigescens*. A. Habit (*Rodríguez 4118*). B. Intersection of petiole, rachis, and pinna-rachises, showing aculei (*Méndez 71*). C. Secondary pinnule, abaxially, showing detail of sori and pseudoindusia (*van der Werff 3040*). D, E *Hypolepis hostilis*. D. Habit of a small frond (*Poeppig s.n.*). E. Secondary pinnule, abaxially (*Cazalet 7707*), showing detail of sori and

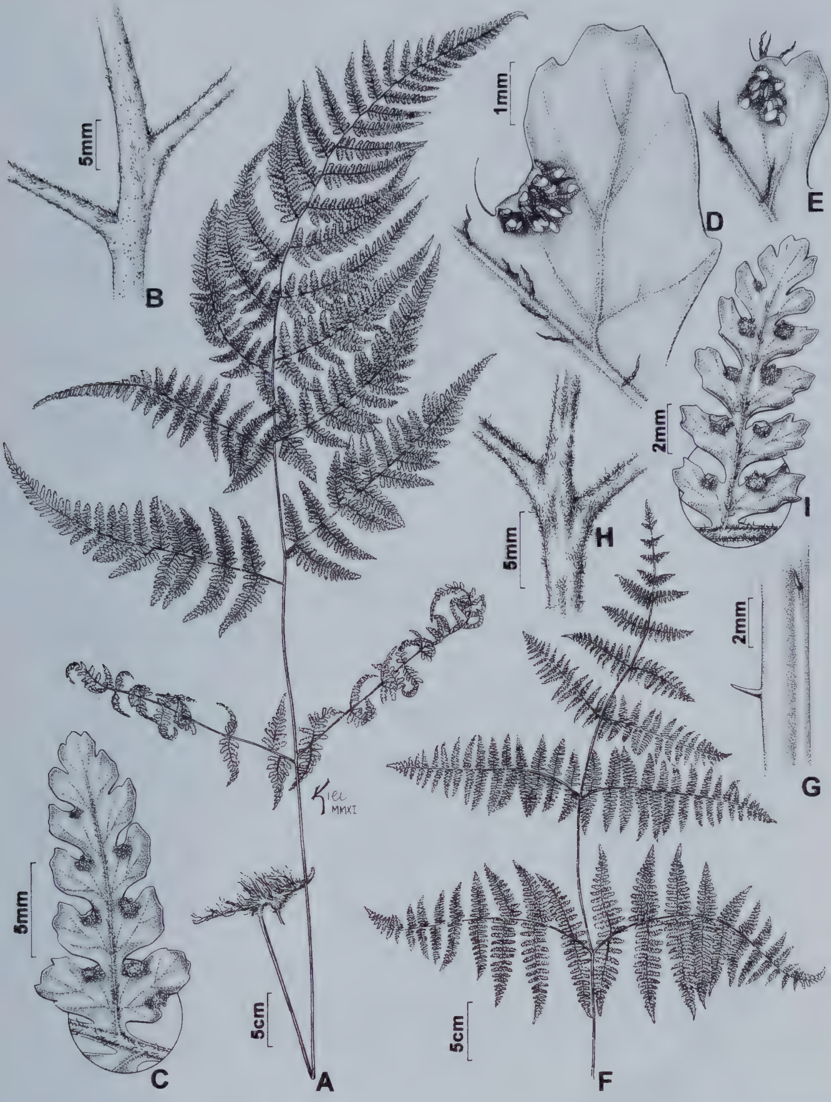

FIG. 13. A–E *Hypolepis poeppigii*. A. Habit (adapted from *Martínez 1879b* and *Cabrera 24186*). B. Intersection of petiole, rachis, and pinna-rachises (*Martínez 1879b*). C. Secondary pinnule, abaxially (*Martínez 1879b*). D. Fertile segment, abaxially, showing detail of slight protected sorus. (*Martínez 1879b*). E. Fertile segment, abaxially, showing detail of submarginal unprotected sorus (*Castellan 12*). F–I *Hypolepis lellingeri* (*Barclay s.n.*). F. Habit. G. Petiole showing aculei. H. Intersection of petiole, rachis, and pinna-rachises. I. Secondary pinnule, abaxially.

←

pseudoindusia. F. *Hypolepis viscosa* (*Moritz 387*), secondary pinnule, abaxially, showing detail of sori and pseudoindusia.

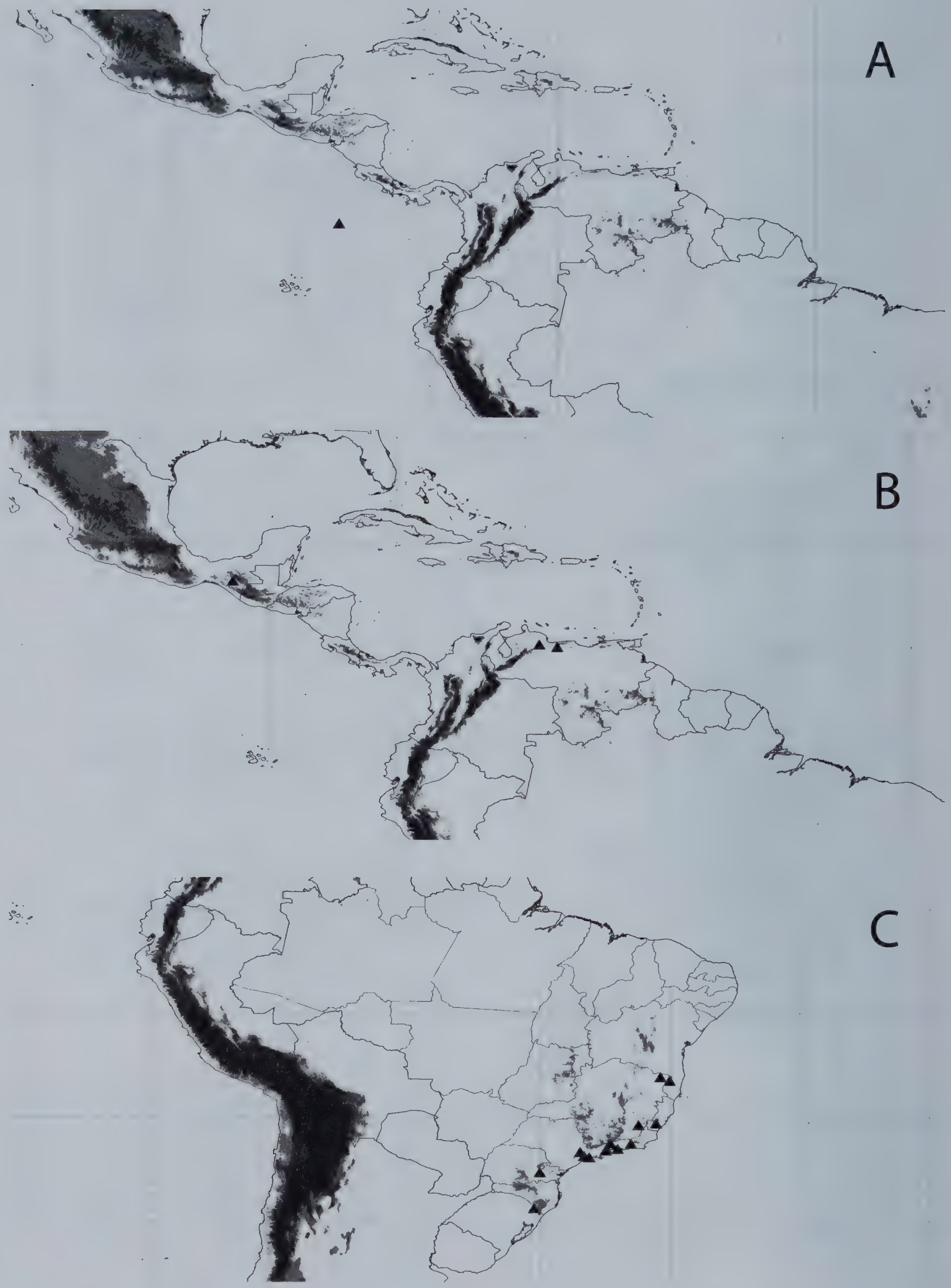

FIG. 14. A. Distribution of *Hypolepis lellingeri*. B. Distribution of *Hypolepis melanochlaena*. C. Distribution of *Hypolepis mitis*.

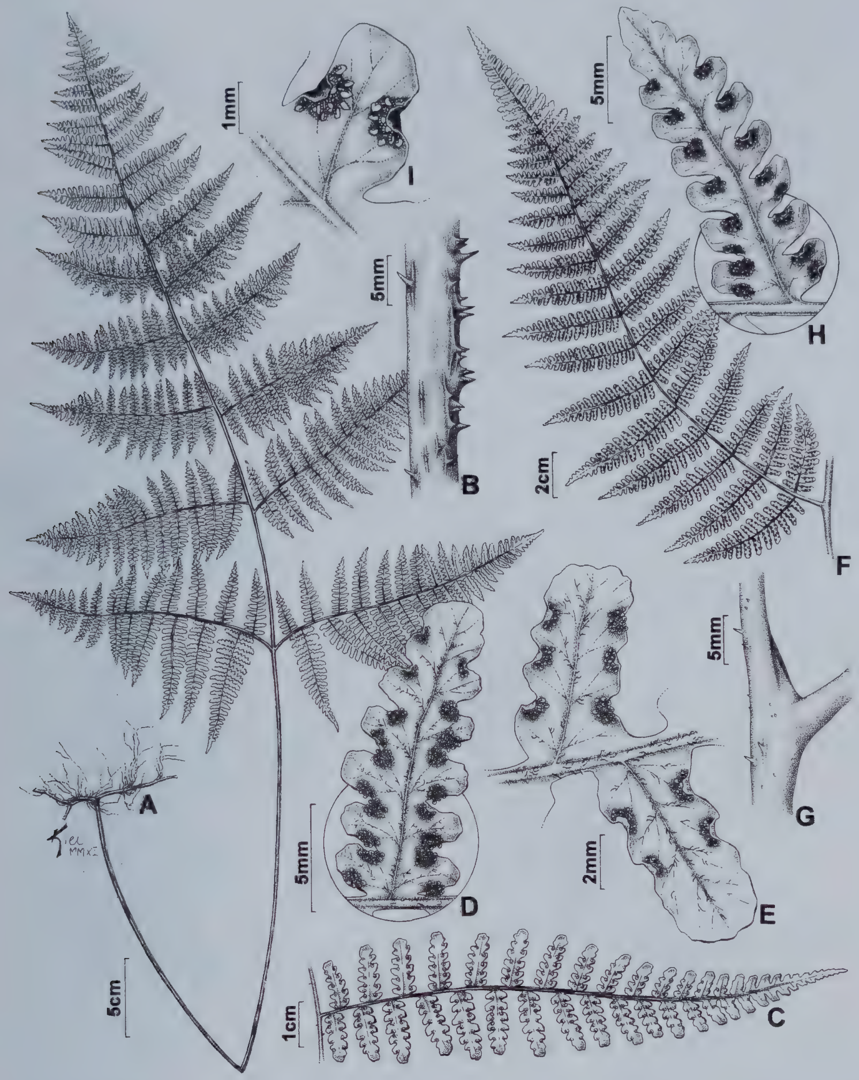

FIG. 15. A–E *Hypolepis repens.* A. Habit of a small frond (*Schwartsburd 2510*). B. Petiole showing aculei (*Schwartsburd 2510*). C. Pinnule, abaxially (*Boudrie 3210*). D. Secondary pinnule, abaxially (*Boudrie 3210*). E. Fertile segments, abaxially, abaxially showing sori and pseudoindusia (*Boudrie 3210*). F–I *Hypolepis melanochlaena.* F. Pinna (*Enrundi 56*). G. Intersection of petiole, rachis, and pinna-rachis, showing aculei (*Trujillo 16492*). H. Secondary pinnule, abaxially (*Enrundi 56*). I. Fertile segment, abaxially, showing detail of sori and blackish pseudoindusia (*Enrundi 56*).

conical shape, and the cells are turgid. After drying the hairs become lax, and take on a true catenate, stair-like appearance, with the cells contracted and twisted at different angles.

Leaves.—The leaves of *Hypolepis* are amongst the largest in the monilophytes. Moran (1995) reported for *H. nigrescens* leaves up to 10 m long; in the

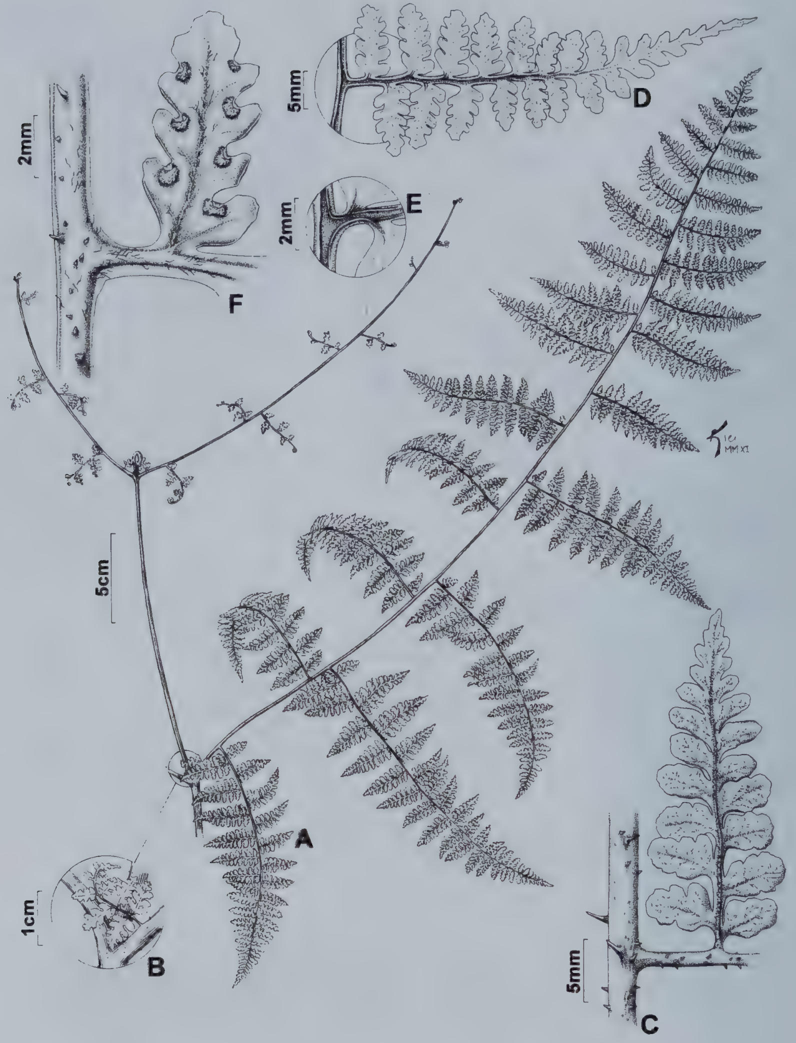

Fig. 16. *Hypolepis nigrescens.* A. Lamina, distally, showing uncoiled apex and intermittent growth (*Rodríguez 5438*). B. Proximal acroscopic pinnule protecting pinna departure (*Rodríguez 5438*). C. Pinna-rachis and secondary pinnule, abaxially, showing aculei (*Atehortúa 1268*). D. Secondary pinnule, adaxially, showing connecting wings (*Rodrígues 5438*). E. Tertially pinnule, adaxially, showing detail of connecting wings (*Rodríguez 5438*). F. Tertially pinnule, abaxially (*Rodríguez 5438*).

present work, a specimen of *H. acantha* was recorded with leaves up to 6.5 m long (*Schwartsburd 1344;* see Fig. 6A). Similar frond sizes can be reached by other Dennstaedtiaceae genera, such as *Blotiella, Dennstaedtia, Histiopteris, Microlepia,* and *Pteridium,* thus being a common feature in the family (*e.g.,* Navarrete and Øllgaard 2000; Schwartsburd *et al.* 2014; Tryon and Stolze 1989).

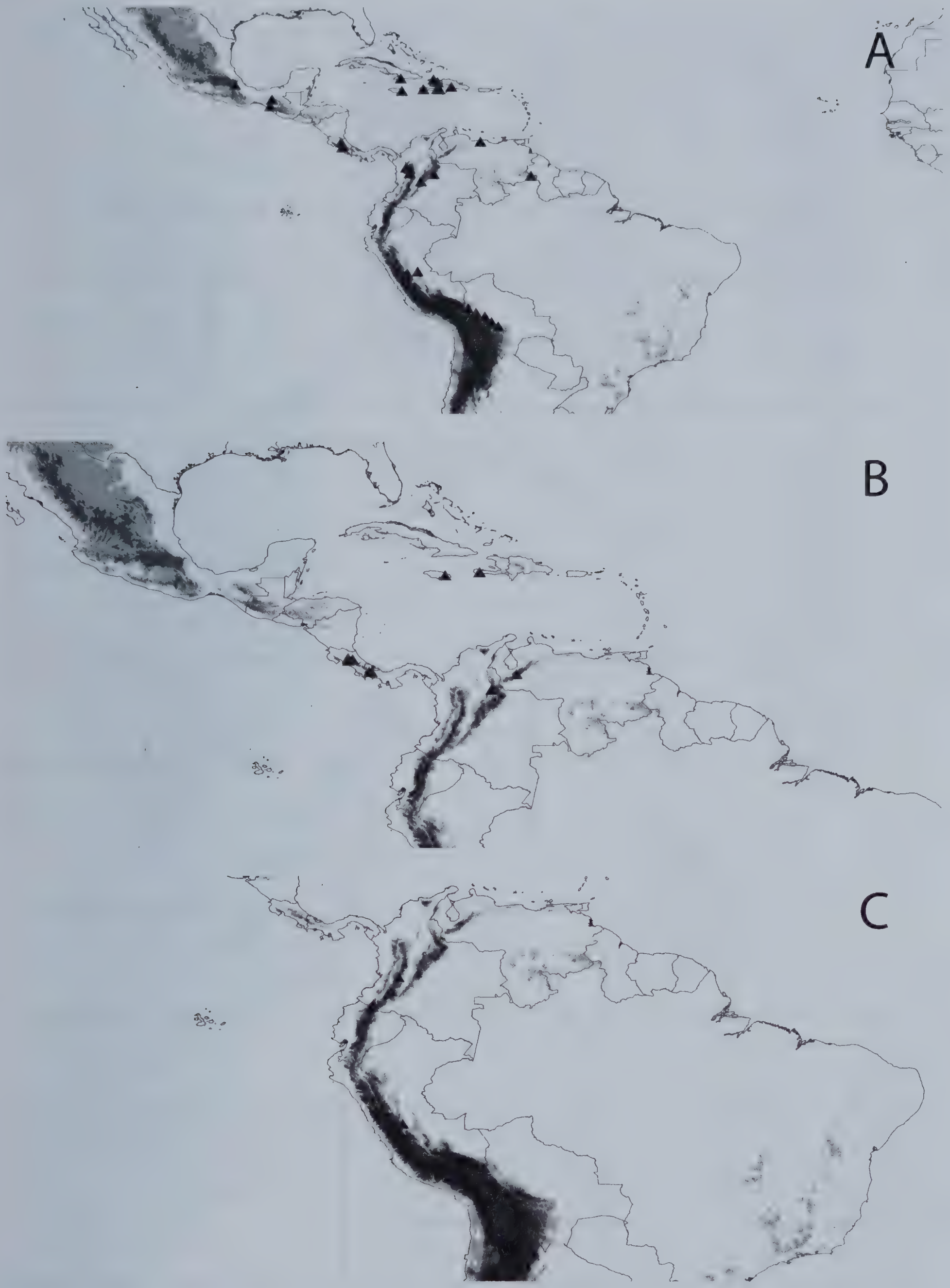

Fig. 17. A. Distribution of *Hypolepis nigrescens*. B. Distribution of *Hypolepis nuda*. C. Distribution of *Hypolepis obtusata*.

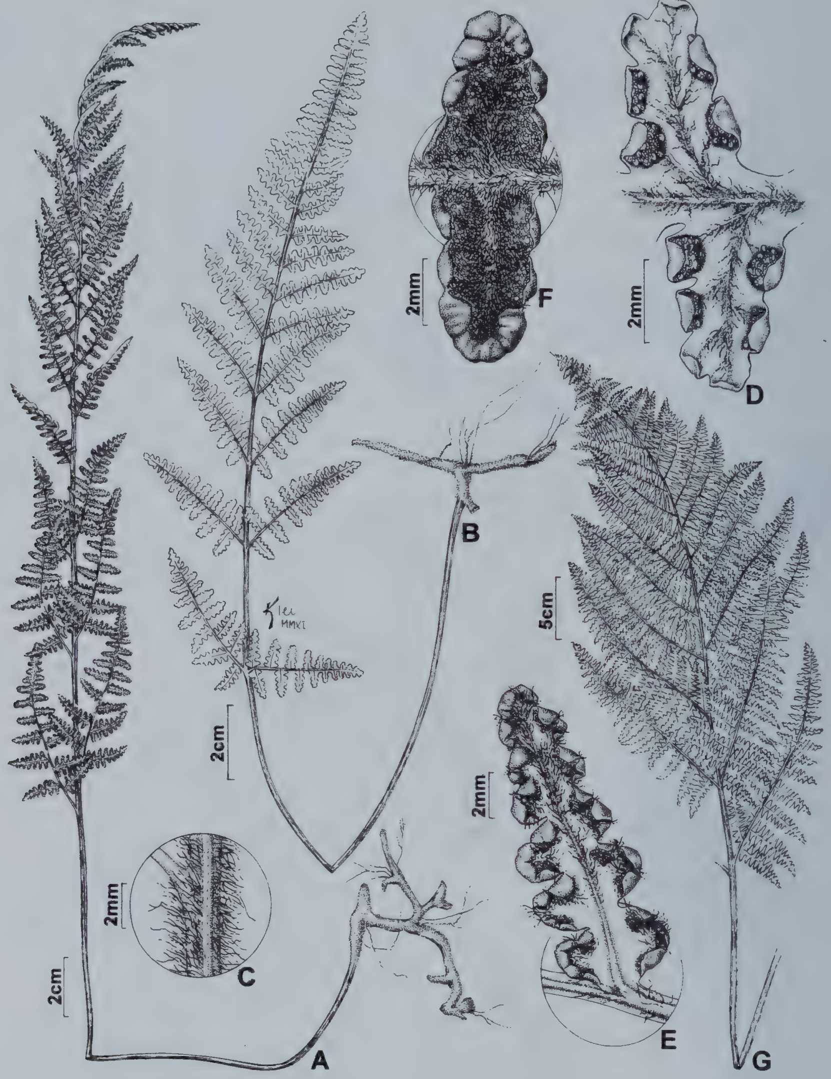

FIG. 18. A–F *Hypolepis obtusata*. A. Habit (*Jiménez 2781*). B. Habit (*Jiménez 2802*). C. Intersection of petiole and rachis, showing lanose axes (*Jiménez 2781*). D. Fertile pinnules, abaxially, showing sori and pseudoindusia (*Jiménez 2802*). E. Fertile pinnule, abaxially (*Jiménez 2781*). F. Fertile pinnules, abaxially, showing "confluent" sori (*Jiménez 2781*). G. *Hypolepis pteroides* (*Lechler 2152*), habit.

Most species of *Hypolepis* have the usual pattern of leaf growth, wherein the apex and lateral pinnae develop at the same time, and the number of pinnae is somehow limited (Figs. 5A, 6D, 8H, 8F, 13A, 13F, 15A, 18A, 18B, 18G, 21A, 24A, 24B). Such regular pattern is here named determinate. On the other hand, some species display intermittent growth where some pinnae are fully expanded while the leaf apex is still developing as a crozier, and producing more pinnae. Virtually, such leaves can grow unlimited and produce an unlimited number of pinnae. This intermittent and indeterminate growth pattern is found in *H. flexuosa* and *H. nigrescens* (Figs. 8A, 16A), and perhaps also in *H. ×glabra*. The intermittent growth is also found in *Paesia* (pers. obs. of the authors), and less related genera, such as *Odontosoria* and in Gleicheniaceae (see Moran 1995, 2004).

Normally, when a *Hypolepis* leaf grows very large, it is no longer self-supporting; rather, the leaves become scandent and are supported by the surrounding vegetation. The scandent habit is phenotypically plastic and is generally not expressed under high light exposure, where the leaves remain erect. This same pattern can be found in *Pteridium arachnoideum* subsp. *arachnoideum* (Schwartsburd *et al.,* 2014; Tryon and Stolze 1989; pers. obs. of the authors). The smaller species (*e.g., H. crassa* and *H. obtusata)* probably always have erect to slightly arched leaves.

Petioles and rachises.—From the solenostelic rhizome, the leaves depart with a leaf gap on the upper lateral side (Gwynne-Vaughan 1903). This gap is responsible for the fronds to bear at the base only one almost circular, but interrupted, vascular bundle. This interruption is outside reflected on the adaxial groove (Fig. 5C), which can be seen from the base of the petioles up to the apex of the rachises. On the studied species, the one big vessel becomes split upwards into two to several vascular bundles. We could identify two different shapes of vascular bundles at the base of the petioles, among the four studied species. We named them as Greek letters (upside down, since the groove is adaxial):

The π-shaped (pi-shaped): at the petiole base it looks like the *pi* letter (Fig. 3B), and upwards it becomes fragmented mainly in two vessels, seeming two snakes facing each other (Fig. 3C). This type was found in *Hypolepis rugosula* subsp. *pradoana.*

The Ω-shaped (omega-shaped or mushroom-like): at the petiole base it looks like the *omega* letter or as a mushroom, then, it becomes fractioned upwards into several vessels (Fig. 4A). An early fragment of the vessel, at the base of the petiole is due to epipetiolar root traces (Figs. 5A, B). The Ω-shaped type was found in *Hypolepis acantha, H. repens,* and *H. stolonifera* var. *stolonifera.* The rachises and pinna-rachises of such species also bear Ω-shaped vascular bundles.

The two lateral lines of aerophore in the petioles are clearly visible both externally (Fig. 5C) and internally in cross section (Figs. 4D, E). The cross-section images show the lines of aerophore internally as interruptions of the outer cortex layer (sclerified cells), and filled by connecting parenchymatous tissue, with gaps (an aerenchyma) (Figs. 4D, E). There is no apparent difference between the species studied, regarding the lines of aerophores internally. The drawings of the tangential sections made by Ogura (1972: Fig. 91) for *Onychium japonicum* (Thunb.) Kunze show a high density of stomata in the region of the lines of aerophores, but we have not looked for stomata. Since most *Hypolepis* species occur in wet grounds, it is reasonable to believe that these lines of aerophore are responsible for gas exchange, and for eliminating water through evaporation — see also Davies (1991:118).

Some species have sharp conical emergences of the epidermis on the petioles, rachises, and pinna-rachises (Figs. 4B, 6B, 9B, 13G, 15B, 15G, 16C, 19C, 19G, 21E, 21F). In the general taxonomic literature, such projections have been named as spines, prickles, or aculei. The term adopted here is aculeus (*pl.* aculei; *adj.* aculeate), since they are not vascularized, and they originate from the epidermis and are filled only with the outer cortex (Fig. 4B). Some other species have rounded tips and obtuse emergences. Since they are not pointed and sharp, they are not named here as aculei, but as tuberculous (*pl.* tuberculei; *adj.* tuberculate).

Laminae and basal pinnae.—Hypolepis species generally present highly dissected laminae. In South America, most species present tripinnate to quadripinnate-pinnatifid laminae. A few species (*e.g., H. obtusata, H. rugosula*) can present bipinnate or bipinnate-pinnatifid laminae, and a few others to pentapinnate (*e.g., H. flexuosa, H. nigrescens, H. stolonifera*). Most species can vary the degree of dissection of the fertile laminae, for example, *H. stolonifera* presents quadripinnate-pinnatifid to pentapinnate laminae, or rarely tripinnate-pinnatifid (Figs. 5A, D).

In all species, the basal pair of pinnae is the most dissected pair. Medially, the laminae tend to be less dissected, and distally they are only pinnatifid (or constantly uncoiled in intermittent fronds). The shape of the basal pinnae is of great taxonomic value. They can either be equilateral (basiscopic and acroscopic proximal pinnules equal in size and dissection — *e.g.,* Fig. 24A), subequilateral (basicopic pinnules larger, but equally dissected — *e.g.,* Fig. 9F), or inequilateral (basicopic pinnules larger and more dissected — *e.g.,* Fig. 5A).

Veins, receptacle, sori, and pseudoindusia.—The veins in *Hypolepis* have little taxonomic value. Every species has free veins, which are primarily pinnate; in some species the secondary veins are furcate. The receptacles are formed at the tip of the veins, thus each sorus is served by only one vein. The receptacle (and the sori) can be either marginal (*e.g.,* Figs. 5I, 6F) or submarginal (*e.g.,* Figs. 13E, 24D). Normally, the submarginal sori lack protection, while the marginal are protected by the recurved lamina margin (= pseudoindusia). The pseudoindusia are semi-lunate and they can bear cilia in the margins (*e.g.,* Figs. 5I, 6F); rarely, they also bear hairs on their adaxial surface (in *H. pedropaloensis* — Fig. 21D). Their color can vary and they have taxonomic value.

Bower (1928) presented drawings about a putative vestigial inner indusium in a "*Hypolepis repens*" specimen from Jamaica. We did not have access to Bower's material and could not confirm this feature. Images showing the soral development of both exindusiate and pseudoindusiate *Hypolepis* can be seen in the work of Schölch (2000).

Indument.—As in most Dennstaedtiaceae genera, the indument of *Hypolepis* is formed solely by hairs, lacking any kind of scales. The hairs in *Hypolepis* are always multicellular formed by at least two cells. Some hairs can reach up to 25 cells in a row. They are never furcate or stellate. Most hairs are catenate, *i.e.,* when dried they get a chain-like (or stair-like) aspect, with the cells contracted and twisted at different angles. Some species can also bear trichomidia. The hair cells are ca. 0.1 mm long, while the trichomidia cells are ca. 0.05 mm long. In this work we adopt the following nomenclature for hairs and trichomidia:

Catenate-acicular hairs—catenate hairs with a sharp conical cell at the tip (Fig. 4F; see also Brownsey 1984: Fig. 1, left drawings);
Catenate-glandular hairs—catenate hairs with a spherical glandular cell at the tip (Fig. 3D; see Brownsey 1984: Fig. 1, right drawings);
Acicular hairs—stiff erect hairs with a sharp conical cell at the tip, and formed only by two or three cells (especially found in *Hypolepis acantha, H. grandis, H. pedropaloensis,* and *H. stuebelii*);
Trichomidia—appressed filiform trichomidia (Fig. 4C);
Bacilliform trichomidia—club-like trichomidia (especially found in *Hypolepis nuda*).

Taxonomic Treatment

Hypolepis Bernh., Neues J. Bot. 1(2): 34. 1806 [Nov 1805], based on *Lonchitis tenuifolia* G. Forst., Fl. Ins. Austr.: 80. 1876 [Oct–Nov 1876]. = *Hypolepis tenuifolia* (G. Forst.) Bernh., Neues J. Bot. 1(2): 34. 1806 [Nov 1805]. *Cheilanthes arborescens* Sw., Syn. Fil.: 129, 336. 1806 [Mar–Apr 1806], *nom. nov.* for *Lonchitis tenuifolia* G. Forst. [*non Cheilanthes tenuifolia* (Burm.) Sw., Syn. Fil.: 129. Mar–Apr 1806]. *Phegopteris tenuifolia* (G. Forst.) Keys., Polyp. Herb. Bunge.: 51. 1873. Lectotype (designated by Brownsey and Chinnock 1987: 25).— VANUATU. Tanna, [1772–1775], *G. Forster s.n.* (BM! ["Insulae Oceani Pacifici"]; probable isolectotypes: B!-frag., BM!, GOET, image!).

Cheilanthes Sw. sect. *Hypolepis* (Bernh.) Kunze, Linnaea 23(2): 242. 1850.
Hypolepis Bernh. sect. *Euhypolepis* Hook. & Baker, Syn. Fil.: 129. 1867. Lectotype (designated here).—*Lonchitis tenuifolia* G. Forst. (= *Hypolepis tenuifolia* (G. Forst.) Bernh.).

Plants terrestrial, rarely humiculous-epipetric. *Rhizomes* long-creeping, branched, with two lateral lines of aerophores; *steles* unique, solenostelic, amphiphloic, cylindric or stellar; *hairs* catenate-acicular, lax or rigid, yellowish or reddish-brown, (0.3–)1–3(–4) mm long, (6–)10–30(–35)-celled, sometimes caducous. *Fronds* small to large, 0.25–10 m long, erect, arched, or scandent, with determinate or intermittent growth; *petioles* (6–)15–400 cm x (0.8–)2–15 mm, essentially brown or burgundy, adaxially grooved, with two lateral lines of aerophores, smooth to aculeate, glabrous to lanose; *petiolar vascular bundle* proximally π-shaped or Ω-shaped, dissected above; *laminae* linear-lanceolate, ovate, or rhombic, (7–)15–700 x (2–)10–300 cm, proximally (bipinnate–) bipinnate-pinnatifid to quadripinnate-pinnatifid (–pentapinnate), distally pinnatifid or constantly uncoiled; *rachises* straight or flexuous, smooth to aculeate, essentially stramineous, brown, or burgundy, glabrous to lanose; *pinnae insertions* with or without nectaries, sometimes protected by proximal acroscopic pinnule; *basal pinnae* equilateral, subequilateral, or inequilateral; *pinna axes* smooth to aculeate, glabrous to lanose; *costae* with or without decurrent adaxial wings; *veins* free; *indument* of acicular, catenate-acicular, glandular, or catenate-glandular hairs, bacilliform trichomidia, and/or trichomidia. *Receptacle* supplied by a single vein, at the sinuses; *sori* rounded, marginal or submarginal, protected by a pseudoindusium, by the undifferentiated lamina margin, or not protected; *pseudoindusia* semi-lunate, greenish to hyaline; *spores* bilateral, monolete. *n* = generally 52 or 104, rarely 28, 29, (39?), or 98.

Hypolepis Bernh. (Dennstaedtiaceae) has priority over two later homonyms (Farr *et al.* 1979): *Hypolepis* P. Beauv. ex Lestib. (Essai Cipér.: 33. 1819 — Cyperaceae), and *Hypolepis* Pers. (Syn. Pl. (Persoon) 2: 598. 1807 [Sep 1807] — Rafflesiaceae). *Hypolepis* is characterized by long-creeping rhizomes with distant nodes, with an unique typical solenostele, commonly large fronds (up to 10 m long), commonly armed petioles and rachises, commonly highly dissected laminae (normally, they are tripinnate-pinnatifid at least), indument formed by catenate-acicular and/or catenate-glandular hairs (i.e., multicellular hairs), marginal or submarginal sori, these round, supplied by the tip of a single vein, and commonly protected by a pseudoindusium.

In general, most Dennstaedtiaceae genera present creeping rhizomes furnished with multicellular hairs, large fronds, highly dissected laminae, and submarginal to marginal sori. Among the South American genera, *Hypolepis* differs from *Blotiella, Histiopteris, Paesia,* and *Pteridium* by the receptacles supplied by only one vein (*vs.* receptacles supplied by commisural veins); *Hypolepis* differs from *Dennstaedtia* and *Microlepia* by the absence of true abaxial indusia (*vs.* present).

KEY TO SPECIES AND HYBRIDS OF *HYPOLEPIS* IN SOUTH AMERICA AND COCOS ISLAND

1. Petioles and rachises armed (aculeate)
  2. Fronds intermittent; aculei darker than the axes; pinnae departures protected by proximal acroscopic pinnule; costae adaxially with decurrent wings. . . . . 13. *H. nigrescens*
  2. Fronds determinate; aculei and axes concolours; pinnae departures unprotected; costae without adaxial wings
    3. Abaxial laminar tissue between the veins glabrous
      4. Fronds less than 1.5 m long; petioles black proximally; rachises and pinna-rachises with both catenate-acicular and catenate-glandular hairs
        5. Petioles glabrous; rachises abaxially glabrous, adaxially with hairs 0.1–0.3 mm long, 2–5-celled; veins abaxially and adaxially with glandular hairs; plants from Continental South/Central Americas . . . . 8. *H. hostilis*
        5. Petioles villous; rachises abaxially and adaxially with hairs 0.3–1.0 mm long, 5–12-celled; veins abaxially and adaxially glabrous; plants endemic to Cocos Island . . . . 10. *H. lellingeri*

4. Fronds more than 2 m long; petioles brown or purple proximally; rachises and pinna-rachises with catenate-acicular hairs and/or trichomidia, catenate-glandular hairs absent

6. Costae, costules and veins abaxially with catenate-acicular hairs (each hair cell ca. 0.1 mm long)

7. Petioles dark brown proximally, lighter brown above; petioles and rachises copiously aculeate, not tuberculate; margins of the pseudoindusia glabrous; plants widespread . . . . 21. *H. repens*

7. Petioles purple proximally, greenish stramineous above; petioles and rachises sparsely aculeate and tuberculate; margins of the pseudoindusia commonly ciliate, rarely glabrous; plants endemic to south and southeastern Brazil . . . . 12. *H. mitis*

6. Costae, costules and veins abaxially with trichomidia (each trichomidia cell ca. 0.05 mm long)

8. Laminae rhombic, drying black; pseudoindusia entirely black, or partly black and partly hyaline; plants from Venezuela and Mexico. . .11. *H. melanochlaena*

8. Laminae oblong, drying olive green; pseudoindusia entirely stramineous; plants from the Andes. . . . . 16. *H. parallelogramma*

3. Abaxial laminar tissue between the veins with hairs or trichomidia

9. Fronds less than 1.5 m long; abaxial laminar tissue between the veins with glandular hairs

10. Rachises and pinna-rachises with catenate-acicular and catenate-glandular hairs, lax, 0.1–0.5 mm long, 4–7-celled; plants from Continental South/Central Americas . . . . 22. *H. rigescens*

10. Rachises and pinna-rachises with catenate-acicular and catenate-glandular hairs, lax, 0.1–0.5 mm long, 4–7-celled, plus some rigid catenate-acicular hairs, with reddish apex, 0.5–1.3 mm long, 7–15-celled; plants endemic to the Galapagos Islands . . . . 5. *H. galapagensis*

9. Fronds more than 2.0 m long; abaxial laminar tissue between the veins with catenate-acicular hairs, acicular hairs, or trichomidia

11. Abaxial laminar tissue between the veins with trichomidia (each trichomidia cell ca. 0.05 mm long); margins of the pseudoindusia glabrous; plants endemic to Bolivia. . . . . 24. *H. scandens*

11. Abaxial laminar tissue between the veins with catenate-acicular or acicular hairs (each hair cell ca. 0.1 mm long); margins of the pseudoindusia usually ciliate, rarely glabrous

12. Petioles and rachises sparsely aculeate and tuberculate; laminar tissue between the veins abaxially strigose; plants from southern and southeastern Brazil . . . . 12. *H. mitis*

12. Petioles and rachises copiously aculeate; laminar tissue between the veins abaxially hirsute

13. Rachises and pinna-rachises with catenate-acicular, acicular, and catenate-glandular hairs; margins of the pseudoindusia copiously ciliate; plants from Peru, Ecuador, Colombia, and Venezuela . . . . .26. *H. stuebelii*

13. Rachises and pinna-rachises with catenate-acicular and acicular hairs, catenate-glandular absent; margins of the pseudoindusia glabrous, rarely with one or two cilia; plants from eastern Brazil. . . . 1. *H. acantha*

1. Petioles and rachises unarmed (sometimes tuberculate, but not aculeate)

14. Fronds intermittent

15. Hairs of the rhizomes 0.3–0.6 mm long, 6–12-celled; fronds usually more than 2 m long; plants from western South America and Central America. . . . . . 4. *H. flexuosa*

15. Hairs of the rhizomes 1–2(–3) mm long, 15–30(–40)-celled; fronds less than 1 m long; plants endemic to the Bogotá Cordillera in Colombia . . . . .6. *H. ×glabra*

14. Fronds determinate

16. Sori unprotected or protected by the undifferentiated lamina margins
17. Petioles sparsely tuberculate, otherwise smooth; rachises and pinna-rachises glabrous; plants from northern South America and Central America . . . . . 14. *H. nuda*
17. Petioles and rachises copiously rugose, not tuberculate; rachises and pinna-rachises with catenate-acicular and catenate-glandular hairs
18. Petioles burgundy; basal pinnae equilateral; veins abaxially and adaxially pubescent; plants from central and southern Argentina and Chile (including Chiloé and Juan Fernandez), and from southern and southeastern Brazil . . . . 23. *H. rugosula*
18. Petioles dark brown proximally, lighter brown above; proximal pinnae subequilateral; veins abaxially and adaxially glabrous; plants from Bolivia, and northern/central Argentina and Chile. . . . . .19. *H. poeppigii*
16. Sori protected by pseudoindusia
19. Costae and costules abaxially lanose, with long, lax catenate-acicular hairs, (0.7)1–3 mm long, (10–)15–35-celled; plants from the Andes, occurring at elevations higher than 3400 m
20. Laminae bipinnate to bipinnate-pinnatifid proximally; basal pinnae 2.5–4.5 x 1.2–2 cm; plants from the Andes. . . . . 15. *H. obtusata*
20. Laminae tripinnate-pinnatifid; basal pinnae 6–20 x 3–12 cm
21. Laminae linear-lanceolate; basal pinnae 6–15 x 3–7 cm; costae and costules abaxially with catenate-acicular hairs 0.7–1 mm long, 10–15-celled; plants endemic to the Andes of Ecuador. . . . . 3. *H. crassa*
21. Laminae ovate; basal pinnae 15–20 x 5–12 cm; costae and costules abaxially with catenate-acicular hairs 1–2 mm long, 15–25-celled; plants from the Andes (Colombia, Ecuador, and Peru). . . . . 20. *H. pteroides*
19. Costae and costules abaxially glabrous to villous, not lanose, with trichomidia or hairs no longer than 1.5 mm long, 15(–17)-celled; plants from the Andes and elsewhere, occurring at elevations lower than 3100 m
22. Abaxial laminar tissue between the veins glabrous
23. Rachises and pinna-rachises with catenate-acicular hairs; basal pinnae inequilateral; plants from southern and southeastern Brazil and northeastern Argentina.. . . . . 25. *H. stolonifera*
23. Rachises and pinna-rachises with catenate-acicular and catenate-glandular hairs; basal pinnae subequilateral
24. Petioles and rachises sparsely tuberculate; adaxial laminar tissue between the veins with trichomidia; plants endemic to Mount Roraima. . . . . 9. *H. krameri*
24. Petioles and rachises not tuberculate; adaxial laminar tissue between the veins glabrous; plants endemic to southeastern Brazil . . . . 17. *H. ×paulistana*
22. Abaxial laminar tissue between the veins with hairs or trichomidia
25. Abaxial laminar tissue between the veins with trichomidia (each trichomidia cell ca. 0.05 mm long)
26. Petioles and rachises sparsely rugose, not tuberculate, with catenate-acicular hairs; basal pinnae 9–18 x 3–10 cm, subequilateral; abaxial laminar tissue between the veins with trichomidia; plants endemic to the Andes of Colombia. . . . . 2. *H. bogotensis*
26. Petioles and rachises tuberculate, otherwise smooth, glabrous; basal pinnae 20–45 x 10–30 cm, inequilateral; abaxial laminar tissue between the veins with bacilliform trichomidia; plants from northern South America and Central America. . . . . 14. *H. nuda*
25. Abaxial laminar tissue between the veins with acicular, catenate-acicular, or glandular hairs (each hair cell ca. 0.1 mm long)
27. Abaxial laminar tissue between the veins with catenate-acicular or acicular hairs

28. Petioles tuberculate; rachises and pinna-rachises with catenate-acicular, acicular, and catenate-glandular hairs; abaxial laminar tissue between the veins hirsute, with acicular hairs; plants endemic to the Andes of Colombia . . . . 18. *H. pedropaloensis*
28. Petioles not tuberculate; rachises and pinna-rachises with catenate-acicular hairs; abaxial laminar tissue between the veins strigose, with catenate-acicular hairs; plants from southern and southeastern Brazil, and northeastern Argentina. . . . . 25. *H. stolonifera*

27. Abaxial laminar tissue between the veins with glandular hairs
    29. Adaxial laminar tissue between the veins glabrous; lamina margins glabrous; margins of the pseudoindusia with glandular cilia; plants endemic to Mount Roraima. . . . . .7. *H. guianensis*
    29. Adaxial laminar tissue between the veins with hairs; lamina margins with hairs; margins of the pseudoindusia with catenate-acicular cilia
        30. Rachises and pinna-rachises with catenate-acicular hairs 1–1.2 mm long, 13–17-celled; veins and laminar margins with catenate-glandular hairs; adaxial laminar tissue between veins with glandular hairs; plants from the Andes of Colombia and Venezuela, and Hispaniola. . . . . . .28. *H. viscosa*
        30. Rachises and pinna-rachises with catenate-acicular hairs 0.2–0.5 mm long, 4–7-celled; veins and laminar margins with catenate-acicular and catenate-glandular hairs; adaxial laminar tissue between veins with catenate-acicular hairs; plants endemic to Mount Roraima . . . . 27. *H. trinationalis*

THE SOUTH AMERICAN SPECIES, SUBSPECIES, VARIETIES, AND *HYBRIDS* OF HYPOLEPIS (INCLUDING COCOS ISLAND)

1. ***Hypolepis acantha*** Schwartsb., Kew Bull. 67(4): 816, Figs. 1A–C, 3A, B. 2012. TYPE.—BRAZIL. **Paraná:** Antonina, Reserva Rio Cachoeira (SPVS), Floresta Ombrófila Densa, 100 m, 26 June 2007, *P.B. Schwartsburd & F.B. Matos 1344* (holotype: SP!-on 4 sheets; isotypes: B!-on 3 sheets, FI!-on 2 sheets, G!-on 3 sheets, K!-on 3 sheets, LP-frag., NY!-on 4 sheets, P!-on 3 sheets, PRC!-on 3 sheets, RB!-on 3 sheets, VIC!-on 3 sheets). **Figs. 6A–C, 7A.**

Plants terrestrial. *Rhizomes* 3.5–7 mm diam.; *hairs* catenate-acicular, yellowish-brown, 1–2 mm long, 15–20-celled. *Fronds* determinate, scandent, (1.7–)3–6.5 m long; *petioles* (0.8)1.5–4 m x (5–)6.5–10 mm, dark brown proximally, lighter brown above, the *aculei* conspicuous, straight, 0.5–2.5 mm long, commonly with a hair at the tip, the *trichomidia* appressed, ca. 0.2 mm long, 4-celled; *laminae* rhombic, quadripinnate-pinnatifid proximally, (1.1–)1.7–2.5 x (1.1–)1.4–2.1 m; *rachises* straight, light brown to brown, aculeate, with trichomidia; *basal pinnae* 55–105 x 35–60 cm, inequilateral; *costae* abaxially and adaxially pilose, the *hairs* catenate-acicular, hyaline with reddish cross-walls, 0.3–0.8 mm long, 6–12-celled; *costules* abaxially pilose, adaxially sparsely pilose, the *hairs* 0.2–0.4 mm long, 3–6-celled; *veins* abaxially pilose, adaxially glabrous; *laminar tissue between the veins* abaxially hirsute, the *hairs* acicular, hyaline, erect, 0.1–0.15 mm long, 1–3-celled, adaxially glabrous; *lamina margins* glabrous; *sori* marginal; *pseudoindusia* proximally greenish, distally hyaline, the *margins* wavy, glabrous or rarely with one or two cilia.

Distribution and ecology.—Endemic to the Atlantic Forest of Brazil (south, southeastern, and northeastern Brazil), especially in *Restingas* (white sand forest); generally from sea level to 100 m elev., but a few records from 1000 m.

Specimens examined.—BRAZIL. **Bahia:** Ilhéus, s.d., *C.F.P. von Martius, Herb. Fl. Bras. 382* (BR-2 sheets). **Espírito Santo:** Linhares, Reserva Florestal de Linhares, Estrada do Louro, 19°05’58”S, 40°02’55”W, 30–60 m, 9 Feb 2007, *T.E. Almeida et al. 687* (BHCB). **Rio de Janeiro:** Rio de Janeiro, Gávea, s.d., *A. Glaziou 5328* (B-2 sheets, K-3 sheets [one *p.p.*]). **São Paulo:** Santo André, Parque Natural Municipal Nascentes de Paranapiacaba, 1000 m, 25 Sep 2009, *P.B. Schwartsburd et al. 2264* (SP, VIC). **Paraná:** Antonina, Reserva Natural do Rio Cachoeira, Trilha dos Pinheiros, 25°18’S, 48°41’W, 30 m, 30 Apr 2006, *F.B. Matos & G. Weiss 1123* (SP, UPCB). **Rio Grande do Sul:** Pelotas, 11 Mar 1956, *A.R.H. Schultz 3648* (ICN).

Due to the armed petioles and rachises, and the strigose abaxial laminar tissue between the veins, *Hypolepis acantha* is morphologically similar to *H. stuebellii,* which occurs in western South America. Besides geography, *H. acantha* differs from *H. stuebelii* by the absence of catenate-glandular hairs (*vs.* present throughout all axes), and by the margins of the pseudoindusia being wavy, glabrous or rarely with one or two cilia (*vs.* margins copiously ciliate) (Fig. 6C *vs.* Figs. 21G, H).

Another species somewhat similar to *Hypolepis acantha,* which also occurs in eastern Brazil, is *H. mitis. Hypolepis acantha* differs from *H. mitis* by petioles and rachises copiously aculeate and non-tuberculate (*vs.* sparsely aculeate and tuberculate), the abaxial laminar tissue between the veins hirsute (*vs.* strigose), with conspicuous, acicular, erect hairs 0.1–0.15 mm (*vs.* sparse, decumbent, catenate-acicular hairs 0.2–0.3 mm long) (Figs. 6A–C *vs.* Figs. 9C–E).

2. ***Hypolepis bogotensis*** H. Karst., Fl. Columb. 2: 91, t. 147, figs. 1, 2, 5. 1865. LECTOTYPE (designated here).—Fl. Columb. 2: t. 147, figs. 1, 2, 5. 1865!; EPITYPE (designated here).—COLOMBIA. **[Cundinamarca** and **Distrito Capital]**: Bogotá, 2800 m, s.d., *A. Lindig 224* (B!-20 0074561-*p.p.* [ex Herb. Mettenius]; isoepitypes: B!-frag. [20 0074561 *p.p;* ex Herb. Kuhn], BM!-*p.p.* [labelled “b” by A.R. Smith], K!-2 sheets, P?). **Figs. 7B, 8H, I.**

Hypolepis bogotensis H. Karst. ex Mett. *in* Triana & Planchon, Ann. Sci. Nat., Bot., ser. 5, 2: 238. 1864, *nom. nud.*

Plants terrestrial or humicolous-epipetric. *Rhizomes* 2–3 mm diam.; *hairs* catenate-acicular, reddish-brown, 1–2(–3) mm long, 15–30(–40)-celled. *Fronds* determinate, erect, 40–90 cm long; *petioles* 15–50 cm x 2–4 mm, light brown, inermous, sparsely rugose, glabrous abaxially, sparsely pilose adaxially, the *hairs* catenate-acicular, hyaline with reddish cross-walls, 0.3–0.7 mm long, 7–10-celled; *laminae* ovate, tripinnate to tripinnate-pinnatifid proximally, 25–50 x

18–32 cm; *rachises* straight, light brown proximally, stramineous distally, inermous, sparsely rugose, glabrous abaxially, sparsely pilose adaxially; *basal pinnae* 9–16 x 3–5 cm, subequilateral; *costae* glabrescent abaxially, sparsely pilose adaxially; *costules* abaxially and adaxially with reddish *trichomidia*, 0.2–0.3(–0.5) mm long, 5–10-celled; *veins* abaxially and adaxially with trichomidia; *laminar tissue between the veins* abaxially and adaxially with conspicuous trichomidia; *sori* marginal; *pseudoindusia* proximally greenish, distally yellowish, glabrous or rarely with trichomidia adaxially, the *margins* smooth, glabrous.

Distribution and ecology.—Endemic to the Bogotá Cordillera, in Colombia (Cundinamarca and Distrito Capital), in wet forests of rocky mountains; from 2400 to 3000 m.

Specimens examined.—COLOMBIA. Nova Granada. **Cundinamarca and Distrito Capital:** Below Alto de Cuchuco, 7 km Southwest of Sibate, 2600–2650 m, 19 Oct 1961, *R.M. Tryon & A.F. Tryon 6129* (GH-*n.v.*, K); Páramo de Coachí, al comenzar el descenso hacia el oriente, ca. 3000 m, 11 July 1974, *C.E. Acosta-Arteaga et al. 579* (COL-*n.v.*, U).

Hypolepis bogotensis is endemic to Bogotá Cordillera, and it is characterized by its thin rhizomes (2–3 mm diam.) with catenate-acicular hairs 1–2(–3) mm long, 15–30(–40)-celled, determinate fronds less than 1 m long (Fig. 8H), inermous petioles and rachises with catenate-acicular hairs 0.3–0.7 mm long, 7–10-celled, and costules, veins, and laminar tissue between the veins with trichomidia only (hairs totally absent). Plants from South America previously referred as "*Hypolepis bogotensis*" (for example, by Murillo-Pulido *et al.* 2008; Navarrete 1999, 2008; Smith and Todzia 1989; Tryon 1964; Tryon and Stolze 1989) are better re-classified as *H. flexuosa;* plants from Central and North Americas previously ascribed to *H. bogotensis* are better re-classified as either *H. flexuosa, H. thysanochlaena,* or to undescribed taxa (see discussion of *H. flexuosa*).

The Karsten collection housed in LE, and cited as "type" by Tryon (1964) must not be considered the type of *Hypolepis bogotensis.* It strongly disagrees with the protologue and the original illustration (Karsten 1865). In fact, the true type of *H. bogotensis* is now lost — thus we here choose as lectotype the original illustration and we also designate an epitype. Other Karsten collections housed in B and W are the type of his *"H. bogotensis* var. *glabra",* which we regard as *H.* ×*glabra* (further details under it).

Hypolepis bogotensis differs from *H. flexuosa* by thinner rhizomes, 2–3 mm diam. (*vs.* 4–10 mm), with catenate-acicular hairs 1–2(–3) mm long, 15–30(–40)-celled (*vs.* hairs 0.3–0.6(–1) mm long, 6–12(–15)-celled), determinate fronds less than 1 m long (*vs.* intermittent fronds up to 6 m long), tripinnate to tripinnate-pinnatifid laminae (*vs.* quadripinnate-pinnatifid to pentapinnate), and costules, veins, and laminar tissue between the veins with trichomidia (*vs.* with catenate-acicular and catenate-glandular hairs, or glabrescent) (Figs. 8H, I *vs.* Figs. 8A–G). Apparently, *H. bogotensis* crosses with *H. flexuosa* generating the hybrid *H.* ×*glabra* (Fig. 8J) (further details under it).

3. ***Hypolepis crassa*** Maxon, Contr. Gray Herb. 165: 69, pl. 4. 1947. Type.—ECUADOR. Imbabura Province, on headwaters of east fork of Río Desaguadero, northwest slopes of Cayambe, ca. 3840 m (12800 ft), 10 July 1944, *I.L. Wiggins 10386* (holotype: US!-1859521, isotype: DS, image!). **Figs. 7C, 9J–L.**

Plants terrestrial. *Rhizomes* 2–5 mm diam.; *hairs* catenate-acicular, yellowish-brown, 1–2 mm long, 15–20-celled. *Fronds* determinate, erect, 45–70 cm long; *petioles* ca. 20–35 cm x 2–3(–5) mm, reddish-brown, inermous, rugose, glabrescent; *laminae* linear-lanceolate, tripinnate-pinnatifid proximally, 30–40 x 12–22 cm; *rachises* mainly straight, but slightly flexuous distally, reddish-brown proximally, stramineous distally, inermous, rugose, glabrescent or sparsely lanose abaxially and adaxially, the *hairs* catenate-acicular, lax, hyaline with reddish cross-walls, 0.7–1 mm long, 10–15-celled; *basal pinnae* 6–15 x 3–7 cm, equilateral; *costae* abaxially sparsely lanose, adaxially glabrescent; *costules* abaxially sparsely lanose, adaxially glabrous; *veins* abaxially sparsely lanose, adaxially glabrous; *laminar tissue between the veins* abaxially and adaxially glabrous; *lamina margins* glabrous; *sori* marginal; *pseudoindusia* green, the *margins* crenate to dentate, glabrous.

Distribution and ecology.—Endemic to the Andes of Ecuador, in the Paramos vegetation; from 3800 to 3850 m.

Specimens examined.—ECUADOR. **Napo:** Road Quito-Baeza, 7–8 km NW of Laguna de Papallacta, Páramo de Guamaní, 00°19'S, 78°08'W, 3800 m, 20 July 1976, *B. Øllgaard & H. Balsev 8155* (AAU-*n.v.*, HB, K). **Tungurahua:** Cordillera de los Llanganates, saddle between Río Topo and Río Verde Grande, on W slope of Cerro Hermoso, 2.4 km from the summit, 01°13'S, 78°18'W, 3850 m, 10 Nov 1980, *L. Holm-Nielsen & J. Jaramillo 28361* (AAU-*n.v.*, K, QCA-*n.v.*, QNA-*n.v.*, U).

Hypolepis crassa is similar to *H. obtusata* and *H. pteroides* due to the short fronds (up to 1 m long), lanose lamina axes, and similar habitat: elevations higher than 3400 m, in the Andes. *Hypolepis crassa* differs from *H. obtusata* by the laminae tripinnate-pinnatifid proximally (*vs.* bipinnate to bipinnate-pinnatifid), 12–22 cm wide (*vs.* (2–)3.5–11 cm), hairs of lamina axes 0.7–1 mm long, 10–15-celled (*vs.* (1–)2–3 mm, (10–)15–35-celled), and marginal sori (*vs.* submarginal) — Figs. 9J–L *vs.* Figs. 18A–F. See comparison with *H. pteroides* under this species.

4. ***Hypolepis flexuosa*** Sodiro, Crypt. Vasc. Quit.: 634. 1893. Lectotype (first step designated by Tryon 1964: 36; second step designated here).—ECUADOR. Crece en las pendientes occidentales del volcán el Corazón, 2800–3000 m, Oct 1891, *A.L. Sodiro s.n.* (P-00633382, image!; isolectotypes: G!-on 2 sheets [00048254], P-00633383, image!, SI-006396, image!, SI-006397, image!). **Figs. 8A–G, 10A.**

Hypolepis repens (L.) C. Presl var. *inermis* Hook., Sp. Fil. 2: 64. 1852, as "*β.*? *inermis*". *Hypolepis inermis* (Hook.) H. Christ, Bull. Herb. Boissier, ser. 2, 4(11): 1095. 1904. Lectotype (designated here).—COLOMBIA. New Grenada, 1844–1846, *W. Purdie s.n.* (K! [labeled as "holotype" by Schwartsburd]; isolectotypes: BM! [ex Herb. J. Sm.], K!, US!-frag.).

Plants terrestrial. *Rhizomes* 4–10 mm diam.; *hairs* catenate-acicular, yellowish brown, 0.3–0.6(–1) mm long, 6–12(–15)-celled. *Fronds* intermittent, scandent, (1–)2–6 m long; *petioles* (0.5–)1–3 m x (4–)7–15 mm, purplish proximally, light reddish-brown above, inermous, rugose, lanose to glabrescent abaxially and adaxially, the *hairs* catenate-acicular, hyaline with reddish cross-walls, or entirely yellowish, lax, 0.2–0.4 mm long, 4–8-celled; *laminae* broadly ovate, quadripinnate-pinnatifid to pentapinnate proximally, (0.5–)1–3 x (0.6–)1–3 m; *rachises* flexuous, light reddish-brown proximally, stramineous above, inermous, rugose, lanose to glabrescent; *basal pinnae* (30–)50–150 x (20–)40–70 cm, inequilateral; *costae* abaxially and adaxially lanose to rarely glabrescent, with two kinds of hairs, the *first kind of hair* catenate-acicular, hyaline with reddish cross-walls, or entirely yellowish, rarely entirely hyaline, lax, 0.3–1 mm, 6–15-celled, conspicuous, the *second kind of hair* catenate-glandular, hyaline with reddish cross-walls, lax, 0.2–0.3 mm, 4–6-celled, scattered and often absent; *costules* abaxially and adaxially lanose to glabrescent, with both kinds of hairs or only the first kind; *veins* abaxially and adaxially lanose to glabrescent, with both kinds of hairs or only the first kind, *this* usually smaller, 0.2–0.4 mm long, 4–8-celled; *laminar tissue between the veins* lanose to glabrescent abaxially, glabrous adaxially; *lamina margins* essentially glabrous, rarely with a few scattered hairs; *sori* marginal; *pseudoindusia* proximally greenish, distally hyaline, the *margins* crenate, dentate, or sometimes with one or two cilia, rarely more.

Distribution and ecology.—Costa Rica, Colombia, Ecuador, Peru, and Bolivia; from 2000 to 4050 m. Possibly also in other Mesoamerican Countries and Venezuela (*apud* Moran 1995, as "*H. bogotensis*"), and maybe Jamaica (*apud* Proctor 1985).

Specimens examined.—COSTA RICA. **San José:** Cordillera de Talamanca, lungo la strada tra Cartago e Cerro de la Muerte, Paramos di Cerro de la Muerte, 19 May 1955, *R.E.G. Pichi-Sermolli 4791* (FI-PS). **Cartago:** Interamerican Highway, slope below Hotel La Georgina, 09°33'29"N, 83°43'24"W, 3093 m, s.d. *M. Sundue et al. 1690* (NY-*n.v.*, SP-on 3 sheets).

COLOMBIA. **Cundinamarca and Departamento Capital:** near Bogotá, Jan 1846, *W. Purdie s.n.* (K — syntype of *Hypolepis repens* var. *inermis*?). **Cauca:** Páramo de las Delicias, Central Andes von Popayan, 3200–3500 m, s.d., *F.C. Lehmann 4441* (B, K-on 2 sheets). **Norte de Santander:** Ocaña, Páramos de San Pedro, 10,000–11,000 ft, 1846–1852 [Jan 1851], *L. Schlim 329* (B, G, K, L, W). **Narino**: in silvis prope Boca del Mundo Nuevo, in Monte Cumbal, reise von Pasto nach Tulcan, 3500 m, s.d., *A. Stübel 341* (B-3 sheets, K-on 2 sheets).

ECUADOR. **Azuay:** Sevilla de Oro, old Road 10–12 km N of the village, 02°46'S, 78°37'W, 2750–2850 m, 11 Sep 1976, *B. Øllgaard & H. Balsev 9383* (AAU-*n.v.*, GH-*n.v.*, HB, K-on 2 sheets). **Carchi:** Base of Volcán Chiles, km 34–36 on Road Tulcán-Maldonado, 00°47'N, 77°57'W, 3900–4050 m, 19 May 1973, *L. Holm-Nielsen et al. 5902* (AAU-*n.v.*, K-on 2 sheets). **Esmeraldas:** Crescit in Prov. Esmeraldas ad fl. Siba, [Aug 1904?], *A.L. Sodiro 13/2* (GH [image!], K). **Imbabura:** Hacienda Yura Cruz, 10 km N of Ibarra, 00°22'N, 78°05'W, 3700–3800 m, 25 May 1973, *L. Holm-Nielsen et al. 6502* (AAU-*n.v.*, K-on 2 sheets).

PERU. **San Martin:** Dist. Huallaga, Valley of Rio Apisoncho, 30 km above Jucusbamba, 07°55'S, 77°10'W, 3600 m, 2 Sep 1965, *A.C. Hamilton & P.M. Holligan 547* (K, L).

BOLIVIA. **La Paz:** Prov. J. Bautista Saavedra M., 15 km de Charazani hacia Chullina, 15°10'S, 68°53'W, 3400 m, 5 July 1997, *M. Kessler et al. 10580* (LPB, UC-*n.v.*). **Cochabamba:** Prov. José Carrasco Torrico, 130 km antigua carretera Cochabamba — Villa Tunarí, 17°07'S, 65°36'W, 2000 m, 11 July 1996, *M. Kessler et al. 7191* (LPB-on 2 sheets, UC-*n.v.*).

Hypolepis flexuosa is here considered a variable widespread species, occurring in Central America and western South America, and confined to high elevations. It may represent a species complex (along with *H. muenchii* (H. Christ) Mickel, *H. thysanochlaena* Mickel & Beitel, possibly *H. trichochlaena* Mickel & Beitel, plus undescribed taxa), which we were unable to solve. More complete collections and additional field studies are needed to better understand this complex. Apparently, some specimens (old fronds?) are glabrescent, blurring the interpretation of the taxa within the complex; also the catenate-glandular hairs are intriguing: they are absent in most specimens analyzed, and present in a few, without geographical correlation. *Hypolepis bogotensis* has commonly been confused with *H. flexuosa,* but does not belong to this complex — although they apparently hybridize (see further comments of *H. bogotensis* and *H. ×glabra*).

Hypolepis flexuosa s.l. is characterized by large fronds (to 6 m long) with intermittent growth, inermous petioles and rachises, quadripinnate-pinnatifid to pentapinnate laminae, and commonly lanose leaf axes (Figs. 8A–G). The other South American taxa with intermittent growth are only *H. nigrescens,* which has armed petioles and rachises, and leaf axes essentially with trichomidia (Figs. 16A–F), and possibly *H. ×glabra,* which has fronds less than 1 m long, and also leaf axes with trichomidia (Fig. 8J). In addition, the rhizome hairs of *H. flexuosa* are the shortest amongst the other South American species: 0.3–0.6(–1) mm long, 6–12(–15)-celled.

5. ***Hypolepis galapagensis*** Schwartsb. & J. Prado, ***sp. nov.*** Type.—ECUADOR. Flora Insularum Galapagensium, **[Santa Cruz, Indefatigable Island?]:** Pampa zone near Media Luna, 1750 ft., May 1974, *H.H. van der Werff 955* (holotype: U!-0256186; isotype: MO?). **Fig. 10B.**

Plants terrestrial. *Rhizomes* 1.5–3.5 mm diam.; *hairs* catenate-acicular, rigid, reddish-brown, 1–2 mm long, 10–15-celled, sometimes caducous. *Fronds* determinate, erect to arched, 55–75 cm long; *petioles* 33–37 cm x 2–4 mm, purple proximally, reddish-brown to light brown above, rugose, the *aculei* straight, 0.2–0.6 mm long, glabrescent abaxially, villous adaxially, with three kinds of hairs, the *first kind of hair* catenate-acicular, hyaline with reddish cross-walls, lax, 0.4–1 mm long, 5–15-celled, conspicuous, the *second kind of hair* catenate-acicular, hyaline with reddish cross-walls and apex, or entirely reddish, rigid, 0.5–1.3 mm long, 7–15-celled, sparse, the *third kind of hair* catenate-glandular, hyaline with reddish cross-walls, 0.3–1(–1.2) mm long, 4–8(–12)-celled, moderate; *laminae* rhombic, quadripinnate to quadripinnate-pinnatifid proximally, 25–50 x 30–50 cm; *rachises* slightly curved proximally, otherwise straight, light brown proximally, stramineous distally, aculeate, rugose, glabrescent abaxially, villous adaxially, with the three kinds of hairs; *basal pinnae* 18–25 x 13–18 cm, subequilateral; *costae* villous abaxially and adaxially, with the three kinds of hairs; *costules* abaxially and adaxially with only catenate-glandular hairs, 0.1–0.5(–0.7) mm long, 2–7(–10)-celled; *veins* abaxially and adaxially with glandular hairs, 0.1–0.2 mm long, 2–4-celled; *laminar tissue between the veins* essentially glabrous abaxially, but with a few scattered glandular hairs, glabrous adaxially; *lamina margins* glabrous; *sori* marginal; *pseudoindusia* proximally greenish, distally hyaline, the *margins* usually dentate, glabrous or rarely with one or two cilia.

Distribution and ecology.—Endemic to the Galapagos Islands (Pinta, San Salvador, and Santa Cruz); from 250 m to 750 m.

Etymology.—The specific epithet is a reference for the distribution of the species, which is endemic to the Galapagos Islands.

Specimens examined.—ECUADOR (GALAPAGOS ISLANDS). **Pinta [Abingdon] Island:** fern peat on summit, 2200 ft, June 1975, *H.H. van der Werff 2118* (U). **San Salvador [Santiago, James] Island:** near summit, 2400 ft, Sep 1975, *H.H. van der Werff 2348* (U) **Island Unknown:** ca. 1800–1810, s.d., *Capt. J. Wood s.n.* (K).

This endemic species has been identified as *Hypolepis repens* by Svenson (1938), and as *H. hostilis* by Morton and Wiggins (1971). Although closely related to *H. hostilis,* both are actually distinct. *Hypolepis galapagensis* is unique in having three kinds of hairs in the petioles and rachises, of which the second kind (catenate-acicular, rigid, with the tip reddish, or entirely reddish) is unique. Apart from the indument, *Hypolepis galapagensis* differs from *H. hostilis* by purple petioles bases (*vs.* black proximally), light brown rachises (*vs.* stramineous), and margins of pseudoindusia dentate, glabrous or rarely with one or two cilia (*vs.* crenate, never ciliate).

Hypolepis galapagensis differs from *H. lellingeri* (endemic to Cocos Island) by purple petiole bases (*vs.* black proximally), petioles and rachises with the three kinds of hair (*vs.* two kinds — the reddish tipped are also absent in *H. lellingeri*), and veins with glandular hairs abaxially (*vs.* glabrous abaxially).

6. ***Hypolepis* ×*glabra*** H. Karst. ex Schwartsb. & J. Prado, ***hybr. nov.,*** Latin diagnosis, description and illustration in H. Karst., Fl. Colomb. 2: 91–92, t. 147, Figs. 3, 4. 1865, sub *Hypolepis bogotensis* H. Karst "*variatio β*". TYPE.—COLOMBIA. **[Cundinamarca and Distrito Capital]:** Bogotá, 2900 m, [26 Mar 1859?], *G.K.W.H. Karsten s.n.* (holotype: W! [as "*Hypolepis Bogotensis* Krst.

var. *glabra,* Bogotá, 2900 m, *H. Karsten*"]; isotypes: B!-20 0019935, W! [as "*Hypolepis Bogotensis* Krst. (var. *glabra*), Bogotá, *H. Karsten*"]). **Fig. 8J, 10C.**

Plants terrestrial or humicolous-epipetric. *Rhizomes* 2–3 mm diam.; *hairs* catenate-acicular, reddish-brown, 1–2(–3) mm long, 15–30(–40)-celled. *Fronds* intermittent, arched to scandent, 40–90 cm long; *petioles* 15–50 cm x 2–4 mm, light brown, inermous, sparsely rugose, abaxially glabrous, adaxially sparsely pilose, the *hairs* catenate-acicular, hyaline with reddish cross-walls, 0.3–0.7 mm long, 7–10-celled; *laminae* broadly ovate, tripinnate-pinnatifid proximally, 25–40 x 34–36 cm; *rachises* flexuous, light brown proximally, stramineous distally, inermous, sparsely rugose, abaxially glabrous, adaxially pilose; *basal pinnae* 17–18 x 8–10 cm, subequilateral; *costae* glabrescent abaxially, sparsely pilose adaxially; *costules* abaxially and adaxially with reddish *trichomidia,* 0.2–0.3(–0.5) mm long, 5–10-celled; *veins* abaxially and adaxially with trichomidia; *laminar tissue between the veins* abaxially and adaxially with scattered trichomidia; *sori* marginal; *pseudoindusia* proximally greenish, distally yellowish, glabrous or rarely with trichomidia adaxially, the *margins* smooth, glabrous.

Distribution and ecology.—Endemic to the Bogotá Cordillera, in Colombia (Cundinamarca and Distrito Capital), in wet forests of rocky mountains; from 2400 to 3000 m.

Parentage.—Putative hybrid between *Hypolepis bogotensis* and *H. flexuosa.*

Etymology.—The specific epithet had already been chosen by Karsten, since the sheets (types) are written this way; it refers to the laminar tissue between the veins abaxially and adaxially with scattered trichomidia (*vs.* trichomidia conspicuous in *Hypolepis bogotensis*).

Specimens examined.—COLOMBIA. Nova Granada. **Cundinamarca and Distrito Capital:** Prov. de Bogotá, La Peña, 2700 m, 1851–1857, *J. Triana s.n.* (FI, W); Nuñez, near Sumapaz, 2400 m, 11 June 1952, *M. Køie 4681* (BM, C-*n.v.*).

Karsten had identified this taxon as a variety of his *Hypolepis bogotensis.* In his collections (see types above) he wrote "*Hypolepis bogotensis* var. *glabra*", but in his work (Karsten 1865), he described it as "*Hypolepis bogotensis variatio β*" — not providing an infra-specific epithet, and thus not validly publishing it (McNeill *et al.* 2012). We are here validating his taxon, but as a hybrid: *H.* ×*glabra.*

Hypolepis ×*glabra* is a putative hybrid between *H. bogotensis,* which is endemic to Bogotá Cordillera, and *H. flexuosa,* which is widespread in western South America and also occurs in Bogotá Cordillera. Most collections of *H.* ×*glabra* presents ill-formed sporangia, except for the holotype, which is apparently fertile. *Hypolepis* ×*glabra* presents an intermediate morphology between the two parietals. The similarities between *H.* ×*glabra* and *H. bogotensis* are: thin rhizomes (2–3 mm diam.) with catenate-acicular hairs 1–2(–3) mm long, 15–30(–40)-celled, short fronds (less than 1 m long — Figs. 8H, J), petioles and rachises with catenate-acicular hairs 0.3–0.7 mm long, 7–10-celled, and costules, veins, and laminar tissue between the veins with trichomidia only. On the other hand, *H.* ×*glabra* and *H. flexuosa* share the intermittent growth of fronds and the flexuous rachises, which are uncommon features within the genus (Figs. 8A, B, J).

7. *Hypolepis guianensis* Klotzsch, Linnaea 20: 339. 1847. LECTOTYPE (designated by Cremers and Kramer 1991: 24).—GUYANA. Habitat in Guiana Anglicana, s.d., *R. Schomburgk 1166* (B!-20 0074653). **Fig. 11A.**

Plants terrestrial. *Rhizomes* not seen. *Fronds* complete not seen, determinate; *petioles* not seen, probably inermous and rugose; *laminae* ovate, tripinnate-pinnatifid (or more dissected) proximally, ca. 55 x 40 cm; *rachises* straight, golden-brown proximally, stramineous above, inermous, rugose, villous abaxially and adaxially, with two kinds of hairs, the *first kind of hair* catenate-acicular, hyaline with reddish cross-walls, or entirely yellowish, 1–2 mm long, 15–25-celled, sparse, the *second kind of hair* catenate-glandular, hyaline with reddish cross-walls, 0.2–0.7(–1) mm long, 4–12(–15)-celled, conspicuous; *basal pinnae* ca. 22 x 7 cm, subequilateral; *costae* villous abaxially and adaxially, with the two kinds of hair; *costules* abaxially with only the second kind of hair, adaxially with the two kinds of hair, but the *first kind* shorter, 0.4–0.7 mm long, 6–10-celled; *veins* abaxially and adaxially with only the second kind of hair, and these shorter, 0.1–0.3(–0.5) mm long, 2–5(–10)-celled; *laminar tissue between the veins* abaxially with the second kind of hair, adaxially glabrous; *lamina margins* glabrous; *sori* marginal; *pseudoindusia* proximally greenish, distally hyaline, the *margins* ciliate, the *cilia* catenate-glandular.

Distribution and ecology.—Endemic to the Mount Roraima region, in the intersection of Venezuela, Guyana, and northern Brazil; elevation unknown (probably from 1500 to 2300).

To describe this species, we analyzed only the type collection, which is represented by part of the frond. Further collections are needed to establish a more comprehensive description. *Hypolepis guianensis* is unique among South America species (maybe worldwide?) by having catenate-glandular cilia along the margins of the pseudoindusia. In every other species with ciliate pseudoindusia, the cilia are catenate-acicular (see Figs. 5I, 6F, 8E, 9E, 9I, 12F, 21D, 21H). The combination of the following characteristics also serves to distinguish *H. guianensis*: inermous petioles and rachises, these with long catenate-acicular hairs (1–2 mm long, 15–25-celled), lamina axes furnished with both catenate-acicular and catenate-glandular hairs, laminar tissue between the veins abaxially with short catenate-glandular hairs and adaxially glabrous, and glabrous lamina margins. For further comparisons with *H. krameri* and *H. trinationalis,* see Schwartsburd *et al.* (2012).

8. *Hypolepis hostilis* (Kunze) C. Presl, Tent. Pterid.: 162. 1836. *Cheilanthes hostilis* Kunze, Linnaea 9: 86. 1834. *Hypolepis repens* (L.) C. Presl var. *hostilis* (Kunze) Baker *in* Martius & Eichler, Fl. Bras. 1(2): 383. 1870. LECTOTYPE (designated here).—PERU. Cresc. in flora Huallagae superior, Peruvia fruticetis graminosis raro ad Mission, Tocache, July–Aug 1830, *E. Poeppig,* *diar. n. 1957* (W! [as "Maijnas, Inter frutices, Tocache, July 1830, *Poeppig*"]; probable isolectotypes: K!-000640334, PRC!, US-frag., image!). **Figs. 11B, 12D.**

Hypolepis parviloba Fée, Crypt. Vasc. Brésil 1: 53, t. 20, Fig. 1. 1869. Lectotype (designated by Tryon 1964: 38).—BRAZIL. Brasilia borealis. **Amazonas:** Serra de São Gabriel, prope San Gabriel da Cachoeira, ad Rio Negro, Feb 1852, *R. Spruce 2119* (P-00633386 [ex Herb. Glaziou], image!; isolectotypes: B-20 0074671, image!, B-20 0074672, image!, BM!-000937674, BM!-000937675, BM!-frag. [ex Herb. Christensen], BR! [2 sheets and a frag.], G! [ex Herb. Dellesert], G! [ex Herb. Barbey-Boissier], GH-*n.v.*, K!-on 2 sheets [000640336 and 000640337], LE!, OXF!, NY, image!, P-00633384, image!, P-00633385, image!, RB!-on 2 sheets [6831], RB!-215824 [ex Herb. Fée], U!-frag., US!-828614).

Plants terrestrial. *Rhizomes* 2–3.5 mm diam.; *hairs* catenate-acicular, yellowish-brown, 1–2 mm long, 15–20-celled, sometimes caducous. *Fronds* determinate, erect to arched, (40–)80–110 cm long; *petioles* (25–)30–40 cm x (1.2–)3–5.5 mm, black proximally, stramineous above, glabrous, sparsely rugose, the *aculei* straight, 0.3–1.7 mm long; *laminae* ovate to rhombic, tripinnate-pinnatifid to quadripinnate-pinnatifid proximally, (30–)60–85 x (25–)60–100 cm; *rachises* slightly curved at base otherwise straight, stramineous, copiously aculeate, rugose, abaxially glabrous, adaxially with two kinds of hairs restricted to the groove, the *first kind of hair* catenate-acicular, hyaline, 0.1–0.6 mm long, 2–8-celled, the *second kind of hair* catenate-glandular, hyaline, 0.1–0.5 mm long, 2–7-celled; *basal pinnae* (12–)30–50 x (7–)20–28 cm, subequilateral; *costae* glabrescent abaxially with the *first* and *second kinds of hair*, pubescent adaxially with only the *first kind of hair; costules* abaxially and adaxially pubescent with only the *second kind of hair*; *veins* abaxially and adaxially sparsely pubescent with only the *second kind of hair; laminar tissue between the veins* abaxially and adaxially glabrous; *lamina margins* glabrous; *sori* marginal; *pseudoindusia* proximally greenish, distally hyaline, the *margins* crenate, glabrous.

Distribution and ecology.—Northern region of South America in the lowlands of the Amazon Forest, in French Guiana, Guyana, Venezuela, Colombia, northern Brazil, Ecuador, Peru, and Bolivia; from sea level to 500 m (one collection from 685 m). Also reported from Panama and Costa Rica (*apud* Moran 1995; no material seen). It is likely to be found in Suriname as well.

Specimens examined.—COLOMBIA. **Amazonas-Vaupés:** Río Apaporis, entre el Río Pacoa y el Río Kananarí, Mouth of Pacoa, ca. 250 m, 17 June 1951, *R.E. Schultes & I. Cabrera 12603* (U). **Amazonas:** Río Popeyacá (affluent of Río Apaporis), lower course, 25 Feb 1952, *R.E. Schultes & I. Cabrera 15616* (BM).

VENEZUELA. **[Mérida or Barinas]:** Along stream and steep slopes with patches of primary vegetation, 5 km SW of Dam site on Río Caparo, 31 km ESE of Santa Barbara, ca. 07°41'N, 71°28'W, ca. 100–300 m, 10 Mar 1980, *R. Liesner & A. González 9335* (MO-*n.v.*, VEN). **Apure:** Reserva Florestal San Camilo, selva siempreverde a lo largo de La Quebrada de la Cristalina hasta la vega del

Cerro La Nulita, 250–280 m, 02 Apr 1968, *J.A. Steyermark et al. 101758* (G, MY?, VEN-*n.v.*). **Miranda:** Dept. Paéz, Fila La Tigra, Qda. San Juan, 18 km al SW de Cúpira, 10°04–05'N, 64°45'W, 500 m, 02–07 Sep 1977, *F. Ortega & A. González 389* (MO-*n.v.*, VEN).

GUYANA. **Potaro-Siparuni:** Pakaraima Mountains, Ireng River, 4 km upstream from Kurutuik Falls along Topaima stream, 05°05'N, 60°02'W, 685 m, 27 Oct 1994, *P. Mutchnick et al. 255* (CAY, U, US-*n.v.*).

FRANCE, FRENCH GUIANA. **Cayenne:** Montagnes de la Trinité, Inselberg Nord-Ouest, 200 m, 18 Jan 1984, *J.J. de Granville et al. 6138* (CAY, U, Z-*n.v.*).

ECUADOR. **Santiago-Zamora[Morona Santiago]:** Taisha, 1500 ft, 07 Feb 1962, *P.C.D. Cazalet & T.D. Pennington 7707* (B-*n.v.*, BM-*n.v.*, K-on 2 sheets, NY-*n.v.*, US-*n.v.*).

PERU. **Loreto:** Provincia de Mcal. Ramon Castilla, ca. 3 km south of the village of Hanta, 03°17'S, 71°51'W, ca. 15 m, 16 Sep 1992, *H. Tuomisto et al. 5227* (AMAZ-*n.v.*, TUR-*n.v.*, U).

BOLIVIA. **Cochabamba:** Prov. Chapare, San Rafael, 500 m, 10 Nov 1966, *R.F. Steinbach 477* (LPB, U, UC-*n.v.*).

Hypolepis hostilis is easily recognized by the following combination of characters: fronds medium sized, (40–)80–110 x (25–)60–100 cm, petioles black proximally, stramineous distally, rachises stramineous, both aculeate and rugose, costae, costules and veins with catenate-glandular hairs, mostly 0.1–0.4 mm long, 2–6-celled, laminar tissue between the veins glabrous abaxially, lamina margins glabrous, and glabrous margins of the pseudoindusia (Figs. 12D, E).

The most similar species are *Hypolepis galapagensis, H. lellingeri, H. rigescens, H. tenerrima,* and *H. viscosa,* and they probably form a natural group within *Hypolepis.* For differentiation between these taxa, see their respective discussion (comments of *H. tenerrima* in *H. rigescens*).

9. *Hypolepis krameri* Schwartsb., Boudrie & Cremers, Fern Gaz. 19(1): 3, Fig. 2B. TYPE.—Intersection of VENEZUELA, GUYANA, and BRAZIL. Mt. Roraima, base of cliff, Oct 1884 — Jan 1885, *E.F. im Thurn 161, Mt. Roraima Exped.* (holotype: BM! [as "set B"]; isotypes: K! [as "set A"], US!-74710). **Fig. 11C.**

Plants terrestrial. *Rhizomes* not seen. *Fronds* complete not seen, determinate; *petioles* not seen; *laminae* probably rhombic, tripinnate-pinnatifid (or quadripinnate-pinnatifid?) proximally, at least 65–70 x 30–46 cm; *rachises* straight, light golden-brown proximally, stramineous above, copiously rugose, the *tuberculei* obtuse, 0.2–0.3 mm long, glabrescent abaxially, sparsely pilose adaxially with two kinds of hair, the *first kind of hair* catenate-acicular, hyaline with reddish cross-walls, 0.2–0.5 mm long, 3–7-celled, the *second kind of hair* catenate-glandular, hyaline with reddish cross-walls, 0.2–0.5 mm long, 3–7-celled; *basal pinnae* ca. 18–23 x 6.5–10 cm, subequilateral; *costae* glabrescent abaxially, sparsely pilose adaxially with the *first and second kinds* *of hairs; costules* abaxially with the *first and second kinds of hair,* adaxially with sparse *trichomidia*, these 0.2–0.3 mm long, 3–6-celled; *veins* abaxially and adaxially glabrous or with very scattered trichomidia; *laminar tissue between the veins* abaxially glabrous, adaxially glabrous or with scattered trichomidia; *laminar margins* glabrous; *sori* marginal; *pseudoindusia* hyaline, the *margins* ciliate.

Distribution and ecology.—Endemic to the Mount Roraima region, around the intersection of Venezuela, Guyana, and northern Brazil (known only from the type collection); elevation unknown (probably from 1500 to 2300).

To describe this species, we analyzed only the type collection, which is represented by part of the frond. Further collections are needed to establish a more comprehensive description. *Hypolepis krameri* is an endemic species from Mount Roraima region co-occurring with another two endemic species: *H. guianensis* and *H. trinationalis. Hypolepis krameri* is much less hairy than the other two and can be easily recognized by the following combinations of characteristics: tuberculate petioles and rachises, rachises and costae with catenate-acicular and catenate-glandular hairs, costules and laminar tissue between the veins with trichomidia adaxially, laminar tissue between the veins glabrous abaxially, glabrous lamina margins, and pseudoindusia with ciliate margins. For further comparisons with *H. guianensis* and *H. trinationalis,* see Schwartsburd *et al.* (2012).

10. ***Hypolepis lellingeri*** A. Rojas, Rev. Biol. Trop. 49(2): 439, Figs. 2 a–c. 2001. TYPE.—COSTA RICA. **Puntarenas:** Puntarenas, Parque Nacional Isla del Coco, Isla del Coco, sendero a Cerro Iglesias, entre la base y la punta de Cerro Pelón, 05°31'55"N, 87°06'45"W, 530 m, 18 June 1997, *A. Rojas 3617* (holotype: INB-*n.v.*; isotypes: CR-*n.v.,* MO-*n.v.*). **Figs. 13F–I, 14A.**

Hypolepis hostilis (Kunze) C. Presl var. *major* Hook., Sp. Fil. 2: 69. 1852, as "var. *β major*". LECTOTYPE (designated here).—COSTA RICA. **Cocos Island:** Voyage of H.M.S. Sulphur, 1836–1841, *G.W. Barclay s.n.* [*2201*?] (K!-on 2 sheets; probable isolectotypes: BM!-2 sheets ["1838, *Barclay 2201*"], BM! ["1840"], BM!-on 2 sheets ["Ins. Cocos", without collector], BM!-on 2 sheets ["Panama"], HB!-83826 ["Panama"]).

Plants terrestrial. *Rhizomes* 2–3 mm diam.; *hairs* catenate-acicular, yellowish-brown, 1–2 mm long, 15–20-celled. *Fronds* determinate, erect to arched, 85–110 cm long; *petioles* 35–50 cm x 2–2.5 mm, black proximally, reddish-brown above, rugose, the *aculei* straight, 0.3–1.1 mm long, commonly with a hair at the tip, abaxially and adaxially villous, the *hairs* catenate-glandular, hyaline with reddish cross-walls, (0.1–)0.3–1.0 mm long, (2–)4–12-celled; *laminae* rhombic, tripinnate-pinnatifid to quadripinnate proximally, 50–70 x 40–70 cm; *rachises* straight, light brown proximally, stramineous above, aculeate, rugose, villous abaxially and adaxially; *basal pinnae* 20–35 x 7–10 cm, equilateral; *costae* villous abaxially and adaxially, the *hairs* similar to those from the petioles and rachises but larger, 0.5–1.3 mm long, 8–17-celled;

costules villous abaxially, glabrescent adaxially; *veins* glabrous abaxially and adaxially; *laminar tissue between the veins* glabrous abaxially and adaxially; *lamina margins* glabrous; *sori* marginal; *pseudoindusia* proximally greenish, distally hyaline, the *margins* slightly crenate, glabrous.

Distribution and ecology.—Endemic to Cocos Island; from 50 to 500 m.

Specimens examined.—COSTA RICA. **Cocos Island:** Forêts de la Valée de Wafer, Feb 1902, "*H.P.*" [*H. Pittier*?] *16237* (G).

In the protologue of *Hypolepis hostilis* var. *major,* Hooker (1858 [1852]) stated that the collector was "Banks". This is likely an error, since there are no *Hypolepis* specimens collected by Banks at K. Instead, the collection of Barclay is indeed annotated by Hooker as *"Hypolepis hostilis β".* Thus we choose this material as the lectotype. The several specimens at BM and HB are likely to be duplicates of this collection, but their labels are slightly different (see nomenclatural paragraph above). We consider these specimens as probable isolectotypes. *Hypolepis lellingeri* is similar to *Hypolepis galapagensis, H. hostilis,* and *H. rigescens,* due to medium sized fronds, aculeate petioles, lamina axes with catenate-glandular hairs, and glabrous lamina margins (Figs. 13F–I) — see also comments of *H. galapagensis* and *H. hostilis,* and Figs. 12A–E. *Hypolepis lellingeri* is endemic to Cocos Island and is unique there. Besides geography, *H. lellingeri* differs from those three species by equilateral basal pinnae (*vs.* subequilateral), costae and costules abaxially with longer catenate-glandular hairs, 0.5–1.3 mm long, 8–17-celled (*vs.* 0.1–0.5 mm long, 2–7-celled), and glabrous veins abaxially (*vs.* with glandular hairs) (Fig. 13I *vs.* Figs. 12C, E). *Hypolepis lellingeri* also differs from *H. hostilis* in having villous petioles (*vs.* glabrous), and light brown and abaxially villous rachises (*vs.* stramineous and glabrous abaxially) (Fig. 13H). It differs from *H. rigescens* by glabrous laminar tissue between the veins abaxially (*vs.* with glandular hairs), and glabrous margins of pseudoindusia (*vs.* margins commonly with one or two cilia) (Fig. 13I *vs.* Fig. 12C).

11. ***Hypolepis melanochlaena*** A.R. Sm., Proc. Calif. Acad. Sci., ser. 4, 40(8): 221, Fig. 7D, E. 1975. TYPE.—MEXICO. **Chiapas:** s.d., *G. Münch 35* (holotype: DS-CAS-0002968, image!; probable isotypes: DS-CAS-0003086, image!, US!-1791750). **Figs. 14B, 15F–I.**

Plants terrestrial. *Rhizomes* 2.5–6 mm diam.; *hairs* catenate-acicular, yellowish-brown, 1–2 mm long, 15–20-celled. *Fronds* complete not seen, determinate, at least 1.7 m long; *petioles* complete not seen, at least 85 cm x 6.5–7 mm, dark brown proximally, lighter brown above, sparsely rugose, glabrous abaxially and adaxially, the *aculei* straight, 0.2–1 mm long; *laminae* rhombic, quadripinnate-pinnatifid proximally, ca. 1 x 0.8–1.2 m; *rachises* straight, golden-brown proximally, light brown to stramineous above, copiously rugose, aculeate, glabrous abaxially, adaxially with *hairs* restricted to the groove, these catenate-acicular, hyaline with reddish cross-walls, 0.2–0.4 mm long, 4–6-celled; *basal pinnae* 40–60 x 25–30 cm, subequilateral; *costae* with sparse *trichomidia* abaxially, these hyaline with reddish cross-walls, appressed, 0.15–0.4 mm long, 4–8-celled, strigose adaxially, the *hairs* similar to those from the rachises but longer, 0.3–0.7 mm long, 5–10-celled; *costules* with trichomidia abaxially, strigose adaxially; *veins* with scattered trichomidia abaxially, glabrous adaxially; *laminar tissue between the veins* glabrous abaxially and adaxially; *lamina margins* glabrous; *sori* marginal; *pseudoindusia* entirely black, or proximally black and distally clathrate, the *margins* smooth to crenate, glabrous.

Distribution and ecology.—Disjunct in Mexico (Chiapas; possibly also in Veracruz) and northwestern Venezuela (Lara-*n.v.,* Yaracuy, Aragua, and Barinas-*n.v.*); from 900 to 1450 m.

Specimens examined.—VENEZUELA. **Yaracuy:** Dept. Bruzual, Mun. Campoelías, en la carretera Campoelías-Tierrita Blanca, km 13–14, vertiente Norte, cabeceras del Río Tupe, Sierra de Aroa, entre La Capilla y la quebrada La Tigra, 1300–1450 m, 17 Nov 1980, *B. Trujillo 16492* (MY-on 2 sheets). **Aragua:** Rancho Grande, 1000 m, Aug 1937, *H. Pittier 13849* (K); Rancho Grande, Nov 1953, *"Enrundi" 56* (VEN-35202).

This species was originally described from collections out of Chiapas, Mexico (Smith 1975, 1981). Later, Smith (1985) reported it from Venezuela. Such disjunct distributions were later accepted and commented on by Moran (1995), Mickel and Smith (2004), and Navarrete (2008). Mickel and Smith (2004) also cited questionable material from Veracruz, Mexico (which, according to their comments, would perfectly agree with the concept here adopted for *Hypolepis melanochlaena*). We saw an isotype of *H. melanochalena* at US and it is very similar to the Venezuelan materials. Both the Mexican and Venezuelan specimens are incomplete and scarce, and further collections are needed to understand this species better. A collection from Ecuador (Carchi, 2600 m, *L. Holm-Nielsen et al. 6249* [K-on 2 sheets]) also appears to represent *H. melanochlaena,* but this specimen is too incomplete to be sure.

This species is most similar to *Hypolepis parallelogramma* and *H. scandens,* based on the armed petioles and rachises, and indument similarities (i.e., costae, costules, and veins with trichomidia abaxially). But, *H. melanochlaena* is unique in the genus in having black pseudoindusia (Figs. 13F–I *vs.* Figs. 19A–H). In addition, the lamina dries black, which is quite uncommon in the genus.

12. *Hypolepis mitis* Kunze ex Kuhn, Linnaea 36: 105. 1870. LECTOTYPE (designated here).—BRAZIL. **[Rio de Janeiro]:** Brasilia, Organ Mountains, in dry bushy places, 1838, *G. Gardner 199* (B!-frag. [ex Herb. Kuhn]; isolectotypes: BM!-000937676, FI-W!-214900, G!-2 sheets, K!-000640335, OXF!, PRC!-frag. *p.p.,* RB!-frag. ["*Gardner 551*"], US!-frag., W!). **Figs. 9A–E, 14C.**

Plants terrestrial. *Rhizomes* 2–6 mm diam.; *hairs* catenate-acicular, yellowish-brown, 1–2 mm long, 15–20-celled. *Fronds* determinate, arched to scandent, (0.75–)2–3.5 m long; *petioles* (0.4–)0.75–1.5 m x 4–7.5 mm, purplish proximally, stramineous above, rugose, the *aculei* straight, 0.2–1.5 mm long, inconspicuous, the *tuberculei* 0.2–0.3 mm long, glabrous abaxially, adaxially with appressed *trichomidia* 0.2–0.4 mm long, 4–8-celled; *laminae* rhombic, quadripinnate to quadripinnate-pinnatifid proximally, (0.45–)1.25–2.5 x (0.6–)1–1.4 m; *rachises* straight, greenish stramineous, sparsely aculeate and tuberculate, rugose, with trichomidia; *basal pinnae* (30–)50–70 x (25–)40–50 cm, subequilateral; *costae* sparsely pilose abaxially and adaxially, the *hairs* catenate-acicular, hyaline, 0.3–0.6 mm long, 3–8-celled; *costules* sparsely pilose abaxially, glabrescent adaxially, the *hairs* similar to those from the costae but smaller, 0.2–0.4 mm long, 2–6-celled; *veins* sparsely pilose abaxially, glabrous adaxially; *laminar tissue between the veins* abaxially sparsely strigose to glabrescent, adaxially glabrous; *lamina margins* glabrous; *sori* marginal; *pseudoindusia* proximally greenish, distally hyaline, the *margins* dentate, commonly with one or two cilia, rarely none or more.

Distribution and ecology.—Endemic to southern and southeastern Brazil; from 350 m to 1800 m.

Specimens examined.—BRAZIL. **Minas Gerais:** Araponga, Parque Estadual da Serra do Brigadeiro, trilha para o Pico do Boné, 26 May 2000, *A. Salino et al. 5482* (BHCB). **Espírito Santo:** Castelo, Parque Estadual do Forno Grande, trilha para o Forninho, 20°30'58"S, 41°05'01"W, 1100 m, 12 Feb 2008, *P.H. Labiak et al. 4545* (CEPEC-*n.v.,* MBML, RB-*n.v.,* UPCB-on 2 sheets). **Rio de Janeiro:** Guapimirim, Parque Nacional da Serra dos Órgãos, Sede Guapimirim, em frente à entrada do Parque, 22°29'37"S, 43°00'05"W, 350 m, 08 Jan 2011, *P.B. Schwartsburd et al. 2317* (FI, K, LP-frag., RB, SP, VIC). **São Paulo:** Mun. Jundiaí, Serra do Japi, na trilha à esquerda antes de chegar na base da Reserva, indo para a Cachoeira Paraíso, 23°14'S, 46°56'W, 996 m, 13 Nov 2009, *J. Prado et al. 2057* (SP, VIC). **Paraná:** Ponta Grossa, Parque Estadual de Vila Velha, interior da maior Furna, 10 June 2004, *P.B. Schwartsburd & F.B. Matos 231* (MBM, UPCB). **Rio Grande do Sul:** Bom Jesus, Capão na Fazenda Caraúna, s.d., *J. Dutra 261 p.p.* (ICN).

The syntypes of *Hypolepis mitis* represent at least two different species. *Lindberg 587* is a collection of *H. stolonifera, Gardner 199* is a collection of *H. mitis s. str.,* and *Burchell 2360* represents a glabrescent form of *H. mitis.* We choose as lectotype the collection of *Gardner 199* (B) because it fits best the protologue. Fée wrote "*Gardner 551*" on the isolectotype in RB, but this is probably due to an upside-down original label. In FI-W the original label with Gardner's number is also upside-down and the number "9" is written in an "open manner" such the number "199" might be construed as "551" (or "661"). In every other aspect these specimens agree with those correctly numbered "199".

Hypolepis mitis can be easily recognized by armed petioles and rachises, and laminar tissue between the veins strigose abaxially, but some specimens are glabrescent in this region, and sometimes seeming glabrous (see Figs. 9C–E). Such specimens may be confused with *H. repens.* Apart from the strigose abaxial laminar tissue, *H. mitis* can be differentiated from *H. repens* by petioles purplish proximally and stramineous above (*vs.* dark brown proximally, lighter brown above), petioles and rachises sparsely aculeate and tuberculate (*vs.* copiously aculeate), and pseudoindusia commonly with one or two cilia, rarely with none or more (*vs.* pseudoindusia never ciliate) — Figs. 9A–E *vs.* Figs. 15A–E.

Hypolepis mitis differs from *H. stolonifera* by petioles and rachises sparsely aculeate and tuberculate (*vs.* inermous), and pseudoindusia commonly with only one or two cilia, rarely with none or more (*vs.* copiously ciliate) — Figs. 9A–E *vs.* Figs. 5A–I, 6D–F. For differentiation with *H. acantha,* see comments of this species.

13. *Hypolepis nigrescens* Hook., Sp. Fil. 2: 66, t. 90C, Figs. 1–3. 1858 [1852; tabula published in 1851], *nom. cons.* Lectotype (designated by Proctor 1985: 179).—JAMAICA. [Catherine's Peak, scandent on trees], [15 Feb], *N. Wilson s.n.* [*555*] (K [not found]; isolectotypes: BM!-000605263, P, image!; probable isolectotype: B!-20 0074711). **Figs. 16A–F, 17A.**

Dennstaedtia rubicaulis H. Christ, Bull. Herb. Boissier, sér. 2, 5(3): 258. 1905. Type.—COSTA RICA. Avec *Pteris anfractusosa* couvrant les arbres de moyenne taille en liane au bord des forêts à Navarro, Costa Rica, [1400 m], [1901–1905], *I. Werckle s.n.* (holotype: BAS? or P, image!; isotypes: US, image!, NY-frag., image!, S, image!).

Hypolepis hispaniolica Maxon, J. Wash. Acad. Sci. 14(4): 88. 1924. Type.—HAITI. Vicinity of Furcy, 1300 m, open slopes of Morne de Ouésane, 26 May–15 June 1920 [13 June 1920], *E.C. Leonard 4796* (holotype: US!-on 3 sheets [1077327, 1077328, and 1077329]; isotypes: B!, BM!, GH?, NY, image!, US!-1077326).

Plants terrestrial. *Rhizomes* 1.5–5 mm diam.; *hairs* catenate-acicular, yellowish-brown, 1–2.5 mm long, 15–20-celled, sparse to sometimes caducous. *Fronds* intermittent, scandent, 3–5(–10?) m long; *petioles* 1–2.5(–?) m x 3–5(–8) mm, purplish to black proximally, light-brown to brown above, rugose and armed, the *aculei* curved, blackish, 0.5–1.5 mm long, commonly with a hair at the tip, glabrous abaxially, adaxially with scattered hairs and trichomidia restricted to the groove, the *hairs* catenate-acicular, hyaline with reddish cross-walls or entirely reddish, 0.4–1 mm long, 6–12-celled, the *trichomidia* hyaline with reddish cross-walls or entirely reddish, laterally appressed, 0.2–0.3(–0.5) mm long, 5–7(–10)-celled; *laminae* ovate(?), quadripinnate-pinnatifid to pentapinnate proximally, 2–4.5(–7?) x 0.8–1.6(–?) m; *rachises* straight, stramineous to light brown, rugose, armed, abaxially and adaxially essentially glabrous but with scattered hairs and trichomidia, with protecting pinnules over pinnae departures and uncoiled apex; *basal pinnae* 40–80(–?) x 40–60(–?) cm, subequilateral; *costae* abaxially with trichomidia and scattered hairs, adaxially with trichomidia and with wings subintending onto the costules; *costules* with trichomidia abaxially and adaxially, sometimes glabrous adaxially; *veins* with trichomidia abaxially and adaxially, sometimes glabrous adaxially; *laminar tissue between the veins* abaxially and adaxially glabrous, or rarely with scattered trichomidia; *lamina margins* glabrous; *sori* marginal; *pseudoindusia* yellowish, the *margins* crenate to dentate, glabrous.

Distribution and ecology.—Cuba, Jamaica, Hispaniola, central and southern Mexico, Mesoamerica, Colombia, Venezuela, intersection of Venezuela, Guyana, and northern Brazil, Peru, and Bolivia; from (900–)1000 to 2800 m.

Specimens examined.—CUBA. **Prov. Oriente**: Sierra Maestra, La Gran Piedra, ca. 1000 m, 28–29 June 1914, *E.L. Ekman, Pl. Itin. Regnell. III 1642* (B, G, S-*n.v.*).

JAMAICA. **Saint Andrew and Portland:** Hardwar Gap, border of St. Andrew and Portland, 15 May 1945, *A.M. Barry P 65* (FI-PS). **Portland:** Port Royal Mts., Blue Mts., trail from Harwar Gap, 3800–4000 ft, 27 Apr 1961, *K.U. Kramer & G.R. Proctor 1783* (U). **Parish Unknown:** Locality unknown, *Wiles s.n.* (K!-000640340, BM!-000605262 — syntypes of *Hypolepis nigrescens*); id. *W. Purdie s.n.* (K!-000640339 — syntype of *Hypolepis nigrescens*).

HISPANIOLA. **Haiti:** Massif de la Hotte, western group, Torbec, top of M. Formon, 2225–2250 m, 03 Jan 1927, *E.L. Ekman, Pl. Ind. Occid. H 7559* (BM, K, S-*n.v.*). **Santo Domingo:** Prov. Barahoma, 1911, *M. Fuertes 1335b* (B-on 2 sheets, BM, G-on 2 sheets, G-on 2 sheets, K, U, W).

MEXICO. **Veracruz:** s.d., *E. Berge 46* [*7946*?] (LE). **Chiapas:** Cerro del Boquerón, June 1914, *C.A. Purpus 6868'* (B-2 sheets).

COSTA RICA. **Heredia:** Braulio Carrillo National Park, 10°15'N, 84°10'W, 1865 m, 11 Nov 1986, *E. Hennipman et al. 6839* (BR, CR-*n.v.*, K-on 5 sheets, U?). **San José:** Dota, Zona Protectora Cerro Nara, Fila, 09°29'40"N, 84°00'50"W, 900–1000 m, 03 Dec 1997, *A. Estrada 1348* (CR-*n.v.*, K-on 2 sheets).

COLOMBIA. **Antioquia:** Medelín, Corregimiento de San Antonio de Prado, vereda Yarumalito, divisoria de aguas con el Mun. Heliconia, 06°15'03.16"N, 75°42'42.38"W, 2725 m, 27 Oct 2006, *W.D. Rodríguez et al. 6031* (HUA-on 2 sheets). **Cundinamarca and Distrito Capital:** Bogotá, Fusagasugá, 1800 m, s.d., *G.K.W.H. Karsten s.n.* (W). **Boyacá:** Carretera Sogamoso-Pajarito, bosque húmedo al borde del Río Cusiana, 2000 m, 04 Feb 1959, *H. Bischler 1779* (FI-PS, G-on 3 sheets).

VENEZUELA. **Distrito Capital:** Caracas, Apr 1842, *J.J. Linden 516* (BM, BM-frag., BR, G, FI-W [as "*Linden 515*"], K, OXF, W — syntypes of *Hypolepis nigrescens*).

Intersection of VENEZUELA, GUYANA, and BRAZIL. Mt. Roraima, 2300 m, s.d., *G.H.H. Tate 498* (NY [image!]).

PERU. **Huánuco:** Huanuco-Tingo Maria Road, km 456, ca. 2400 m, 13 Apr 1977, *A. Gentry et al. 19308* (AMAZ-*n.v.*, F-*n.v.*, G-on 2 sheets, MO-*n.v.*, USM-*n.v.*).

BOLIVIA. **La Paz:** Saavedra, Camata, Cerro Asunta Pata, entre el Cerro Yuyo y Camata, camino hacia Apolo, 15°05.23'S, 68°29.33'W, 1420 m, 02 Nov 2003, *J.R.I. Wood et al. 19800* (K, USZ-*n.v.*). **Cochabamba:** Prov. Chapare, Territorio Indígena Parque Nacional Isiboro-Secure, Cordillera de Mosetenez, cresta arriba de laguna Carachupa, 16°14'S, 66°25'W, 1550 m, 02 Sep 2003, *M. Kessler et al. 13186* (LPB, UC-*n.v.*).

All the syntypes originally cited by Hooker (1858 [1852]) correspond to *Hypolepis nigrescens* in the present concept, except for *Cuming 271*

(K!-000492487, FI-W!-on 2 sheets, LE!-2 sheets, OXF!-2 sheets, RB!, UPS!), which is a specimen of *Dennstaedtia scandens* (Blume) T. Moore. Hooker and Baker (1868: 130) had already excluded this collection from the syntypes. Schwartsburd and Prado (2009) showed the name *Hypolepis nigrescens* Hook. is a later homonym of *Hypolepis nigrescens* (Schrad.) Nees (Cyperaceae), and had been equivocally used for nearly 150 years. Hooker's name is now a *nomen conservandum* (see Brummit 2011, for more details).

Hypolepis nigrescens is very different from all other American species of *Hypolepis,* and probably deserves generic segregation. Its distinctive characteristics are shared only with the Australasian *H. brooksiae* Alderw., *H. celebica* C. Chr. *in* Kjellberg & C. Chr. (synonym of *H. brooksiae, apud* Brownsey 1987), and *H. scabristipes* Brownsey. These features include intermittent fronds (Fig. 16A), petioles and rachises with curved and blackish aculei (Figs. 16C, F), pinnae departures covered by accessory proximate pinnules (Fig. 16B), and costae with adaxial wings subintending onto the costules (Figs. 16D, E).

Apart from distribution, *Hypolepis nigrescens* differs from *H. brooksiae* and *H. celebica* by segments and lobes with the apexes dentate (*vs.* rounded), and costae, costules, and veins abaxially with trichomidia (*vs.* with catenate-acicular hairs). *Hypolepis nigrescens* differs from *H. scabristipes* by these same differences, and by tough solid aculei, which are persistent (*vs.* fragile, hollow, caducous aculei) (Figs. 16C, F).

14. *Hypolepis nuda* Mett. *in* Kuhn, Linnaea 36: 105. 1870. LECTOTYPE (first step designated by Proctor 1985: 177; second step designated here).—VENEZUELA. **Mérida:** Mérida, s.d., *F. Engel 171* (B!-20 0074725 *p.p.* [ex Herb. Mettenius]; isolectotypes: B!-frag. [20 0074725 *p.p.,* ex Herb. Kuhn], US!-frag.; probable isolectotypes: LE!-2 sheets). **Fig. 17B.**

Plants terrestrial. *Rhizomes* 3.5–9 mm diam.; *hairs* catenate-acicular, yellowish-brown, 1.5–2(–3) mm long, 15–20(–30)-celled. *Fronds* determinate, erect to arched, 0.6–2 m long; *petioles* 15–50 cm x 2.5–5 mm, brown to dark brown proximally, golden-brown above, inermous, non-rugose, glabrous, the *tuberculei* rounded, 0.1–0.15 mm long; *lamina* ovate, tripinnate-pinnatifid to quadripinnate-pinnatifid proximally, 40–150 x 40–130 cm; *rachises* straight, golden-brown proximally, light brown above, inermous, non-tuberculate, non-rugose, glabrous; *basal pinnae* 20–65 cm x 10–30 cm, inequilateral; *costae* abaxially and adaxially glabrescent or with scattered trichomidia, the *trichomidia* bacilliform, appressed, yellowish or reddish, 0.07–0.2(–0.3) mm long, 1–3(–4)-celled; *costules* abaxially and adaxially with sparse trichomidia; *veins* abaxially with sparse trichomidia, adaxially glabrous or with scattered trichomidia, the *trichomidia* similar to those from the costae and costules, but usually smaller, 0.07–0.1 mm long, 1 or 2-celled; *laminar tissue between the veins* with the same indument pattern that of the veins; *lamina margins* glabrous; *sori* submarginal; *pseudoindusia* usually absent, rarely the lamina margins slightly differentiated and partly protecting the sori, then partly green, partly hyaline, the *margins* smooth to slightly crenate, glabrous.

Distribution and ecology.—Jamaica, Hispaniola, Costa Rica, Panama, Colombia, and Venezuela; from 1450 to 2350 m.

Specimens examined.—JAMAICA. **Parish Unknown:** 5000–6000 ft, July 1878, *G.S. Jenman 30* (K, OXF-2 sheets).

HISPANIOLA. **Haiti:** Dep. du Sud, Massif de la Hotte, western group, on the western ridge of La Blanche, 1500 m, 8 Aug 1917, *E.L. Ekman, Pl. Ind. Occid. H 579* (K, S-*n.v.*).

COSTA RICA. **Alajuela:** Forêts de l'Achiote, Volcan du Poas, 2200 m, Nov 1896, *A. Tonduz 10696* (BR, G-2 sheets, LE-2 sheets, US-*n.v.*). **San José:** Forêts du Roble, massif du Volcan de l'Irazu, ca. 2000 m, 10 July 1891, *H. Pittier 4173* (B, BM, BR, G-on 2 sheets, G-2 sheets, US-*n.v.*).

PANAMA. **Chiquiri:** Cerro Punta, Las Nubes, Parque Internacional La Amistad, sendero al Castillo, próximo a la cabaña, 2300 m, 19 Sep 1994, *I. González 55* (K-on 2 sheets [as "*55 a1*" and "*55 a2*"]).

COLOMBIA. **Santander:** "Lisabita", 5 Apr 1879, *W. Kalbreyer 1111* (B-6 sheets).

VENEZUELA. **Mérida:** Mérida, s.d., *G.K.W.H. Karsten s.n.* (W-2 sheets); Mérida, 1859, *F. Engel 103b* (B).

Hypolepis nuda is readily identified by medium-sized fronds, 60–200 x 40–130 cm, furnished only with bacilliform trichomidia (especially on the abaxial surface of veins and laminar tissue between the veins), glabrous, inermous, and non-rugose petioles and rachises, tuberculei present on the petioles (especially proximally), submarginal sori, and pseudoindusia mostly absent. In some specimens, the lamina margins are slightly differentiated into pseudoindusia, but they never protect the whole sori. *Hypolepis nuda* is the unique species in South America with bacilliform trichomidia. Other species from Mesoamerica and Antilles also are characterized by having bacilliform trichomidia, and they probably form a natural group. They are: *H. ekmanii* Maxon (*Ekman, Pl. Ind. Occid. H. 7503* [holotype: US!-1302995; isotype: BM!), *H. trichobacilliformis* R.C. Moran (type not seen), and *H. urbanii* Brause (*Fuertes 1779* [types: B!-200075239, B!-200075241, US!-1167851]).

15. *Hypolepis obtusata* (C. Presl) Kuhn, Festschr. Jubil. Königstädt. Realsch. Berlin: 347 (Chaetopterides: 27). 1882. *Cheilanthes obtusata* C. Presl, Reliq. Haenk. 1: 64, t. 11, Fig. 1. 1830. LECTOTYPE (designated by Tryon 1964: 36).—PERU. Peruanae Montanae, 1790, *T.P.X. Haenke s.n.* (PR!-5735; isolectotype: PRC!-450746). **Figs. 17C, 18A–F.**

Polypodium fulvescens Hook. & Grev. *in* Hooker, Bot. Misc. 2: 239. 1831. LECTOTYPE (designated by Tryon 1964: 36).—PERU, near Pasco, Huaylluay, s.d., *A. Cruckshanks s.n.* (GH-*n.v.*; isolectotypes: K!-2 sheets, US-frag., *n.v.*; probable isolectotypes: B!-frag., LE! [ex Herb. Greville]).

Hypolepis purdieana Hook., Sp. Fil. 2: 69, t. 91, Fig. B. 1852. LECTOTYPE (designated here).—NEW GRENADA [COLOMBIA], Paramo of Ruiz, 1844, *W. Purdie s.n.* (K!-000640330; isolectotypes: BM!, US!-frag.; probable isolectotype: B!-frag.).

Plecosorus peruvianus Fée, Gen. Filic.: 151. 1852. LECTOTYPE (designated by Tryon 1964: 36).—PERU. Habitat in Peruviâ, [Pavon, dedit nobis Matrit. ann. 1809; Donné par Ruiz/Pavon à Madrid en 1809–1810)] *H. Ruiz López & J.A. Pavón y Jimenez s.n.* (K!-frag. [000640333 *p.p.*]; isolectotypes: MA?, OXF!, P?, RB! [ex Herb. Fée]).

Plants humiculous-epipetric. *Rhizomes* 1.5–3.5 mm diam.; *hairs* catenate-acicular, yellowish-brown, 2–3(–4) mm long, 20–30(–35)-celled. *Fronds* determinate, erect, (15–)25–60 cm long; *petioles* 10–25 cm x 0.8–2.8 mm, purplish proximally, reddish-brown above, glabrescent, with sparse hairs similar to those from the rhizomes, inermous, rugose; *laminae* linear-lanceolate, bipinnate to bipinnate-pinnatifid proximally, (7–)15–40 x (2–)3.5–11 cm; *rachises* straight, reddish-brown proximally, stramineous above, inermous, rugose, abaxially and adaxially sparsely lanose, the *hairs* catenate-acicular, lax, hyaline with reddish cross-walls or rarely entirely reddish, (1–)2–3 mm long, (10–)15–35-celled; *basal pinnae* (1.5–)2.5–5.5 x (0.8–)1.2–2.8 cm, subequilateral; *costae* abaxially lanose, adaxially sparsely lanose to glabrescent; *costules* abaxially lanose, adaxially glabrous; *veins* abaxially lanose, adaxially glabrous; *laminar tissue between the veins* glabrous abaxially and adaxially; *lamina margins* glabrous; *sori* submarginal, frequently confluent; *pseudoindusia* slightly differentiated, entirely green, the *margins* smooth to slightly crenate, glabrous.

Distribution and ecology.—Andes of Colombia, Ecuador, Peru and Bolivia, in Paramo vegetation; from 3800 to 4600 m.

Specimens examined.—COLOMBIA. **Tolima:** Tolima, "Hoha" Paramo, 4600 m, s.d., *A. Stübel 70* (B). **Cauca:** Popayan, s.d., *A. Stübel 94* (B); Puracé-Sotará, 3900 m, s.d., *A. Stübel 129* (B). **Nariño:** Azufral de Túquerres, Laguna Verde, s.d., *A. Stübel 315* (B).

ECUADOR. **Carchi:** Road Tulcán-Maldonado, at the base of Volcán Chiles, 34–36 km from Tulcán, 00°47'N, 77°57'W, 3950 m, 2 Aug 1976, *B. Øllgaard & H. Balslev 8374* (AAU-*n.v.*, HB, K, U).

PERU. **Ancash:** Cordillera Blanca, Quebrada Honda, West side of L. Vinouyo on moraine, 4300 m, 26 June 1979, *M. Gibby & P. Barrett 44* (BM). **Pasco:** Huayllay, s.d., *A. Mathews 968* (K, OXF).

BOLIVIA. **La Paz:** Franz Tamayo, Comunidad Kiara (antiguo), en dirección a la laguna Waka qocha, 17 June 2005, *I. Jiménez et al. 2781* (BOLV-*n.v.*, CTES-*n.v.*, HSB-*n.v.*, LPB, MO-*n.v.*, UC-*n.v.*, USZ-*n.v.*).

Hypolepis obtusata is distinctive by occurring at extremely high elevations (3800 to 4600 m), and recognized by its small fronds, (15–)25–60 x (2–)3.5–11 cm, lamina axes with long catenate-acicular hairs, 2–3(–4) mm long, 20–30 (–35)-celled, bipinnate to bipinnate-pinnatifid laminae, ascendant pinnae, revolute lamina margins, confluent sori, and slightly differentiated pseudoindusia, which are entirely green (Figs. 18A–F). Some specimens, apparently the "sheltered forms", have the pinnae slightly ascendant, and the lamina margins flat (Figs. 18B, D *vs.* Figs. 18A, F).

A similar species, which Tryon (1964) and Tryon and Stolze (1989) considered as a synonym, is *Hypolepis pteroides*. *Hypolepis obtusata* differs from *H. pteroides* by hairs of the rhizome being much longer, 2–3(–4) mm long, 20–30(–35)-celled (*vs.* 1–2 mm long, 15–20-celled), shorter fronds, (15–)25–60 x (2–)3.5–11 cm (*vs.* 60–100 x 20–35 cm), linear-lanceolate lamina (*vs.* ovate), which is bipinnate to bipinnate-pinnatifid proximally (*vs.* tripinnate-pinnatifid), submarginal sori (*vs.* marginal), and slightly differentiated pseudoindusia, which are entirely green (*vs.* proximally green, distally hyaline) (Figs. 18A–F *vs.* Fig. 18G). Another similar species is *H. crassa* (see its comments for differentiation).

For figures 19–26, description of species 16–28, Names of Uncertain Application, Excluded Names, Acknowledgments, Literature Cited, and Appendices 1–3, see "A Taxonomic Revision of the South American Species of *Hypolepis* (Dennstaedtiaceae), Part II." American Fern Journal 106(1).

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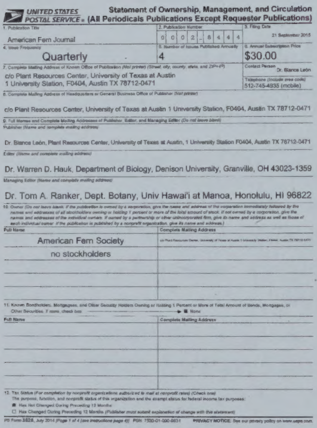

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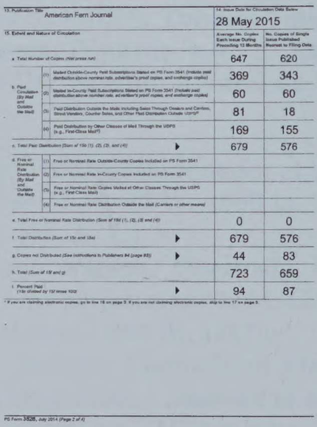

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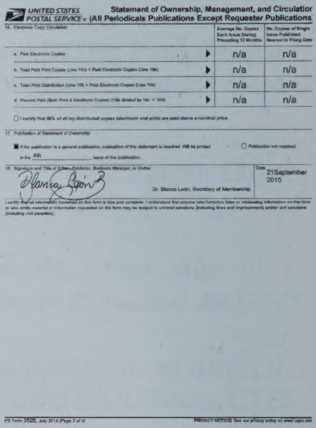

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